

The Honorable Michelle L. Peterson

UNITED STATES DISTRICT COURT
WESTERN DISTRICT OF WASHINGTON
AT SEATTLE

WILD FISH CONSERVANCY, a Washington
non-profit corporation,

Plaintiff,

v.

BARRY THOM, in his official capacity as
Regional Administrator of the National Marine
Fisheries Service; CHRIS OLIVER, in his
official capacity as the Assistant Administrator
for Fisheries of the National Marine Fisheries
Service; NATIONAL MARINE FISHERIES
SERVICE; WILBUR ROSS, JR., in his official
capacity as Secretary of the United States
Department of Commerce; and UNITED
STATES DEPARTMENT OF COMMERCE,

Defendants.

and

ALASKA TROLLERS ASSOCIATION,

Intervenor-Defendant.

No. 2:20-cv-0417-MLP

**DECLARATION OF DR. DANIEL
SCHINDLER IN SUPPORT OF
DEFENDANT-INTERVENOR ALASKA
TROLLERS ASSOCIATION'S BRIEF IN
OPPOSITION TO PLAINTIFF'S MOTION
FOR PRELIMINARY INJUNCTION**

I, DANIEL SCHINDLER, Ph.D., hereby declare as follows on the basis of personal
knowledge to which I am competent to testify:

1. I am 18 years of age and have personal knowledge of the facts contained in this
declaration and am otherwise competent to testify as to matters in this declaration.

2. I am a professor in the School of Aquatic and Fishery Sciences at the University
of Washington. A true and correct copy of my qualifications, including publications, is

1 contained in my curriculum vitae attached as **Exhibit "A"** to this declaration. My research takes
 2 an ecosystem approach to exploring how aquatic systems are organized and respond to changes
 3 in the broader environment. In particular, I am interested in how aquatic ecosystems respond to
 4 change in climate and land-use and interact with fisheries. I pursue most of my current research
 5 in Alaska as a principal investigator of the Alaska Salmon Program, which has studied Pacific
 6 salmon, their ecosystems, and their fisheries in western Alaska since the 1940s. I also pursue
 7 research on aquatic systems in Washington state, where we are interested in how urbanization
 8 and climate change affect ecosystem function and services in this region.

9 3. I participated with my colleague Ray Hilborn in preparing the report of the
 10 Independent Science Panel on the Effects of Salmon Fisheries on Southern Resident Killer
 11 Whales (SRKW) published on November 30, 2012. A true and correct copy of that Final Report
 12 is attached to my declaration and marked **Exhibit "B"**.

13 4. I have been asked by the Alaska Trollers Association to provide an expert opinion
 14 in this matter on issues related to the requested closure of this year's southeast Alaska summer
 15 Chinook troll fishery that the plaintiff Wild Fish Conservancy is seeking in this lawsuit,
 16 ostensibly in order to help survival and recovery of the SRKW.

17 5. In that regard, I have reviewed the Declaration of Dr. Robert Lacy and the
 18 Declaration of Dr. Deborah Giles that were provided to this Court by the plaintiff.

19 6. Attached as **Exhibits C, D, and E**, are the publications referenced below:

- 20 a. *Competing tradeoffs between increasing marine mammal predation and*
 21 *fisheries harvest of Chinook salmon*, Scientific Reports, November 20, 2017;
- 22 b. *Demographic changes in Chinook salmon across the Northeast Pacific*
 23 *Ocean*, Wiley Fish and Fisheries, Original Article, January 17, 2018; and
- 24 c. *Resurgence of an apex marine predator and the decline in prey body size*,
 25 Proceedings of the National Academy of Sciences of the United States of
 26 America (PNAS), November 23, 2019.

7. In addition to drawing upon my knowledge and expertise, I have reviewed and am
 DECLARATION OF DR. DANIEL SCHINDLER IN SUPPORT OF LANDYE BENNETT BLUMSTEIN LLP
 DEFENDANT-INTERVENOR'S BRIEF IN OPPOSITION TO 1300 SW 5th Avenue, Suite 3600
 PLAINTIFF'S MOTION FOR PRELIMINARY INJUNCTION Portland, OR 97201
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1 familiar with the materials cited throughout this declaration.

2 8. In summary, my opinions regarding the relationship between the southeast Alaska
3 summer commercial troll fishery for Chinook salmon and the population status of SRKW are as
4 follows:

5 a. **The Southern Resident Killer Whale (SRKW) population is clearly in**
6 **trouble.** This is a small population, making it vulnerable to extinction based on
7 low abundance alone. There is strong evidence that the population is declining,
8 and nutritional stress appears to be one of several leading candidates as a causal
9 agent of this decline.

10 b. **SRKW are highly dependent on adult Chinook salmon to meet their**
11 **nutritional needs.** An estimate of 525,000 adult Chinook is provided in the
12 declaration by D. Giles as the number of salmon needed to satisfy the annual
13 nutritional needs of the SRKW. Chasco et al. (2017) estimated that 190,000-
14 260,000 adult Chinook salmon were consumed by the SRKW within Salish Sea
15 waters. With either estimate, it is clear that all resident killer whales, including the
16 SRKW, have a high requirement for adult Chinook salmon to meet their
17 metabolic needs (i.e., their predatory demand). While they will eat other species,
18 resident killer whales demonstrate a clear preference for the largest Chinook
19 salmon available to them.

20 c. **The status of SRKW must be considered in the context of recovering marine**
21 **mammal populations along the entire North American west coast of the**
22 **Northeast Pacific Ocean.** The abundance of most marine mammal populations
23 has increased substantially in the coastal Northeast Pacific since the passing of the
24 US Marine Mammal Protection Act in 1972. In particular, Northern Resident
25 Killer Whales (NRKW) have more than doubled in abundance since the 1970s,
26 and have a high degree of dietary overlap with SRKW (i.e., they too, are

specialists on large Chinook salmon). In total, all resident fish-eating killer whales

are estimated to consume at least 2.5M adult Chinook salmon annually in the Northeast Pacific Ocean, most of which is by the NRKW (Chasco et al. 2017). Further, nearly all of the fish eaten are at least three years old (i.e., among the largest in the population).

While the range of NRKW tends to be further north along the west coast (mostly in coastal British Columbia) than the range of SRKW, the primary food of both whale populations is Chinook salmon produced from rivers in the Pacific Northwest (PNW) and coastal British Columbia. Thus, SRKW compete with other resident killer whale populations for their Chinook salmon prey, particularly the NRKW and resident killer whales in the Gulf of Alaska. The total predation rates by all resident killer whales on Chinook salmon returning to rivers in the PNW more than doubled from 1975 to 2015 (Chasco et al. 2017), suggesting that competition between NRKW and SRKW has increased during this time period as well.

- d. **Chinook salmon populations are losing the largest and oldest individuals from populations.** There is a very clear trend in the sizes and ages of Chinook salmon returning to rivers throughout the Northeast Pacific Ocean. In general, Chinook salmon are now younger, and smaller at a given age, than they were four decades ago (Ohlberger et al. 2018). While this trend becomes more pronounced with increasing northerly latitude from northern California to western Alaska, it is clear that a broad scale mechanism must be causing this trend shared among Chinook populations along the entire coastline.

A recent mathematical modeling analysis shows that these changes in Chinook salmon demographic characteristics are not consistent with changes in harvest by size selective fisheries. Instead, these changes in Chinook populations are strongly consistent with the observed changes in the intensity of size-selective predation

by burgeoning resident killer whale populations along the coast (Ohlberger et al.

2019). Though such modeling analyses do not provide definitive proof of any specific mechanism for causing changes in Chinook populations, it does allow for a weight-of-evidence approach for assessing the plausibility of different mechanisms for causing changes in Chinook populations. With regard to observed changes in Chinook sizes and size-at-ages, the weight-of-evidence certainly points to the importance of increasing predation by killer whales at the scale of the Northeast Pacific coast for causing the observed changes in Chinook salmon. This result further strengthens the argument that predation intensity on adult Chinook salmon has increased in the last four decades.

- e. **The Southeast Alaska commercial summer troll fishery catches mostly Chinook salmon that are returning to rivers in the Pacific Northwest.** Based on mixed-stock genetic analysis from Alaska Department of Fish & Game (Gilk-Baumer et al. 2013, 2018), at least 75% of Chinook salmon caught in Southeast Alaska troll fisheries originate from rivers south of Alaska (i.e., British Columbia and the Pacific Northwest). Recognition that this fishery intercepted fish produced from Pacific Northwest rivers formed the basis of the Pacific Salmon Treaty which establishes allowable catches in Alaska waters to ensure sufficient Chinook returns to rivers south of Alaska.
- f. **The Southeast Alaska summer troll fishery captures a small number of Chinook salmon in federal waters, relative to the predatory demand by fish-eating killer whales.** Most of the Chinook salmon caught in the Southeast Alaska Commercial Summer Troll Fishery are caught in Alaska state waters; from 2010-2018, approximately 14% of all Chinook salmon caught annually were from EEZ waters (Table 1).

To put the number of Chinook salmon caught by the Southeast Alaska Summer Troll Fishery in an ecosystem context, I compared these harvest numbers to the

estimated annual predation demand by SRKW (525,000 adult Chinook salmon; D.

Giles declaration) and by all resident fish-eating killer whales in the Northeast Pacific (2.5M Chinook salmon; Chasco et al. 2017). In Table 1 we can see that the number of Chinook salmon caught in EEZ waters of the Southeast Alaska Summer Troll Fishery represents only 5% of the annual predatory demand by SRKW, and about 1% of the annual predation demand by all fish-eating killer whales in the ecosystem. Further, this comparison assumes that the fish caught in this troll fishery would have otherwise survived the migration back to SRKW habitat, which would never happen considering the gauntlet of predators and other fisheries these fish have to migrate through before becoming available to SRKW (see point h below).

Table 1. Number of Chinook salmon caught in the Summer Southeast Alaska Commercial Troll Fishery from 2010-2018. Also given are the numbers caught in federal waters (# in EEZ) and their percentage of the total. Data compiled from the Alaska Department of Fish & Game. The right hand columns express these numbers as a percentage of the annual predatory demand by SRKW, and by all fish-eating killer whales in the Northeast Pacific, for all Chinook caught in the Summer Troll Fishery, and for Chinook caught from the EEZ waters only.

Number of Chinook salmon caught in Summer Southeast Alaska Troll Fishery				All Chinook from Summer SE AK troll fisheries		Chinook from Summer SE AK troll fisheries - EEZ only	
Year	total # caught	# in EEZ	% EEZ	% predation demand by SRKW	% predation demand by all resident KW	% predation demand by SRKW	% predation demand by all resident KW
2010	195,614	29,066	15%	37%	8%	6%	1%
2011	242,193	19,426	8%	46%	10%	4%	1%
2012	209,036	19,502	9%	40%	8%	4%	1%
2013	149,528	11,593	8%	28%	6%	2%	0%
2014	355,570	60,766	17%	68%	14%	12%	2%
2015	269,862	25,525	9%	51%	11%	5%	1%
2016	276,432	33,721	12%	53%	11%	6%	1%
2017	129,525	10,328	8%	25%	5%	2%	0%
2018	107,565	38,889	36%	20%	4%	7%	2%
average	215,036	27,646	14%	41%	9%	5%	1%

g. Genetics data from Chinook salmon caught in the Southeast Alaska EEZ have a

1 **stock composition that is virtually indistinguishable from the stock composition of**
 2 **fish caught in state waters** (Gilk-Baumer et al. 2018). Thus, closing EEZ waters to the
 3 Southeast Alaska Summer Troll fishery would simply displace these fishermen to state
 4 waters where they would likely catch fish destined for the same rivers as in the EEZ.

- 5 h. **Few salmon caught in the Summer Southeast Alaska Commercial Troll Fishery**
 6 **would have otherwise survived to return to PNW rivers.** Chinook salmon caught in
 7 Southeast Alaska troll fisheries otherwise have to migrate through the gauntlet of
 8 predators (particularly the NRKW) and fisheries along the British Columbia coast before
 9 they become available for predation by SRKW. In fact, most killer whale predation on
 10 Chinook salmon occurs by NRKW along coastal British Columbia as Chinook salmon
 11 are migrating back from the Gulf of Alaska to rivers in the PNW. Between 1975 and
 12 2015 the number of adult Chinook salmon eaten by killer whales more than doubled in
 13 this region (Chasco et al. 2017), and resident killer whales are several-fold more
 14 abundant here than in PNW waters.

15 Further, Chinook salmon are subjected to both recreational and commercial fisheries as
 16 they migrate from Southeast Alaska back to rivers in the PNW. Mortality incurred from
 17 these fisheries would add to the mortality resulting from predation by coastal killer
 18 whales during this migration. Thus, simply eliminating the capture of Chinook salmon
 19 from EEZ waters of the Southeast Alaska Commercial Troll Fishery does not produce an
 20 equivalent number of Chinook salmon available to SRKW. The number of fish that
 21 would be spared from the troll fishery in the EEZ and that survived to become available
 22 for predation by SRKW would be distinctly lower than the numbers of fish currently
 23 caught in this fishery.

24 Here I provide, as an example scenario, how a reduction in the number of Chinook
 25 salmon taken in the Southeast Alaska Summer Troll Fishery (i.e., by closing EEZ waters)
 26 would translate into a much smaller number of fish that would eventually be available to

Chinook leaving Southeast Alaska before they would be available as prey to SRKW. Given this reasonable scenario, the number of fish that would be produced by closing EEZ waters and become available to SRKW would equate to about 1.01% of the annual dietary requirement of the SRKW population (see calculations below).

- (i) Number of Chinook not caught in the EEZ in summer troll fishery (Table 1) = 27,646
- (ii) Number of Chinook caught in state waters by fishing effort being displaced there, assuming a 50% reduction in effective effort = 13,823
- (iii) Number of additional Chinook leaving SE AK = 13,823
- (iv) Number of additional Chinook leaving SE AK bound for rivers in PNW, assuming 80% of fish originate from PNW Chinook stocks (Gilk-Baumer et al. 2018) = 11,508
- (v) Number Chinook caught in Canadian fisheries (assuming 20%) = 2,212
- (vi) Number Chinook eaten by NRKW (assuming 20%) = 2,212
- (vii) Number of Chinook reaching PNW waters (iv – v – vi) = 6,635
- (viii) Number Chinook caught in PNW fisheries before reaching SRKW (assuming 20%) = 1,327
- (ix) Number Chinook surviving to become available to SRKW (vii – viii) = 5,308
- (x) Percent of annual SRKW dietary needs this represents = $5,308 / 525,000 = 1.01\%$

- i. **Functional relationships linking SRKW population demographics to changes in Chinook salmon abundance are extremely uncertain.** The declaration provided by R. Lacy shows the output from a mathematical model to predict the responses of SRKW populations to changes in the abundance of Chinook salmon available to them. The functional relationships linking SRKW demographic rates to Chinook prey abundance are extremely uncertain, are based on weak correlations, and should be considered as speculative. While the evidence is relatively convincing that SRKW are suffering because of reduced abundance of their Chinook salmon prey, the quantitative nature of this relationship is very poorly constrained.
- Further, the model simulations are presented in the Lacy declaration as point estimates of the SRKW population through time. A proper simulation would show the cloud of lines that would be produced if the model properly accounted for all uncertainties in the functional relationship between Chinook abundance and SRKW demographics. I think it is likely that the cloud of lines produced from each model scenario would overlap highly

with other scenarios of Chinook salmon abundance; these clouds produced from different scenarios are very unlikely to be statistically distinguishable.

The application of the model used in the R. Lacy declaration should be viewed as a heuristic exercise, not as specific predictions about how SRKW will respond to changes in Chinook abundance. Doing the latter is misleading about the state of our knowledge of the ecology of SRKW in an ecosystem context.

9. Conclusion: In my professional opinion, and for the reasons and facts described above, I believe that a closure of the EEZ waters of the Southeast Alaska Summer Troll Fishery for Chinook salmon would increase the amount of prey available for SRKW by only a trivial amount. While it is clear that SRKW are highly dependent on Chinook salmon for meeting their nutritional requirements, the commercial troll fishery in EEZ waters of Southeast Alaska is a minor threat to the feeding ecology, and likely the population status, of the SRKW.

References

- Chasco, B.E., I. Kaplan, A.C. Thomas, A. Acevedo-Gutierrez, D.P. Noren, M.J. Ford, M.B. Hanson, J.J. Scordino, S.J. Jeffries, K.N. Marshall, A.E. Shelton, C. Matkin, B.J. Burke, & E.J. Ward. 2017. Competing tradeoffs between increasing marine mammal predation and fisheries harvest of Chinook salmon. *Scientific Reports* 7, 15439.
- Gilk-Baumer, S., W.D. Templin, and L.W. Seeb. 2013. Mixed stock analysis of Chinook salmon harvested in Southeast Alaska commercial troll fisheries, 2004-2009. Alaska Department of Fish and Game, Fishery Data Series No. 13-26, Anchorage.
- Gilk-Baumer, S., D.F. Evenson, K. Shedd, and E.L. Jones. 2017. Mixed stock analysis of Chinook salmon harvested in Southeast Alaska commercial troll and sport fisheries., 2016. Alaska Department of Fish and Game, Fishery Data Series No. 18-01, Anchorage.
- Ohlberger, J., D.E. Schindler, E.J. Ward, T.E. Walsworth, and T.E. Essington. 2019. Resurgence of an apex marine predator and the decline in prey body size. *Proceedings of the National Academy of Sciences, USA* 116: 26682-26689.
- Ohlberger, J., E.J. Ward, D.E. Schindler, and B. Lewis. 2018. Demographic changes in Chinook salmon across the Northeast Pacific Ocean. *Fish and Fisheries* 19: 533-546.

10. Pursuant to 28 U.S.C. § 1746, I declare under penalty of perjury that the foregoing is

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1 true and correct to the best of my knowledge.

2 Executed on May 8, 2020, at Seattle, Washington.

3 

4 DANIEL SCHINDLER

Curriculum Vitae

May 6, 2020

DANIEL EDWARD SCHINDLER

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University of Washington
Box 355020
Seattle, WA 98195-5020
Telephone 206-616-6724; FAX 206-685-7471
Email: deschind@uw.edu

1. Personal data

Birth date: 25 January 1968;
Place of birth: Peterborough, Ontario, Canada;
Citizenship: dual U.S.A./Canada

2. Education

Ph.D., Zoology (1995)
University of Wisconsin, Madison, WI.

M.S., Zoology (1992)
University of Wisconsin, Madison, WI.

B.Sc., Biology - Honours (1990)
University of British Columbia, Vancouver, B.C.

3. Research Interests

Aquatic ecosystems; Aquatic biogeochemistry; Climate change and ecosystem dynamics; Food web ecology; Riparian – aquatic coupling; Sustainable fisheries; Watershed ecology

4. Ph.D. Dissertation Title

The role of fishes in habitat coupling in lakes (James F. Kitchell, major professor, 1995)

5. Employment

Professor	School of Aquatic and Fishery Sciences, University of Washington (April 2008 – present)
Associate Professor	School of Aquatic and Fishery Sciences, University of Washington (September 2003 – April 2008)
Associate Professor	Department of Biology, University of Washington (September 2002 – 2008)
Visiting Associate Professor	Department of Ecology and Evolutionary Biology, Cornell University (October 2005 – May 2006)
Assistant Professor	Department of Zoology, University of Washington (September 1997 – August 2002)
Adjunct Asst. Professor	School of Aquatic and Fishery Sciences, University of Washington (May 2001 – September 2003)

Research Associate	Center for Limnology, University of Wisconsin (December 1995 - July 1997)
Research Assistant	Center for Limnology, University of Wisconsin (September 1991 - December 1995)
Teaching Assistant	Department of Zoology, University of Wisconsin (September 1990 - May 1991)
Research Technician	Department of Fisheries and Oceans, West Vancouver, BC (1988 – 1990)
Research Technician	Department of Fisheries and Oceans, Winnipeg, MB (1985 – 1987)

6. Selected Honors and Awards

- 1) G. Evelyn Hutchinson Award from the Association for the Sciences of Limnology and Oceanography, 2020. (<https://www.aslo.org/aslo-awards/2020-aslo-award-recipients/2020-hutchinson-award-recipient/>)
- 2) Elected Member of the Washington State Academy of Sciences (2018 – present)
<https://environment.uw.edu/news/2018/07/aquatic-and-fishery-sciences-daniel-schindler-elected-to-the-washington-state-academy-of-sciences/>
- 3) Frank H. Rigler Award, highest honour from the Canadian Society of Limnologists, January 2015. (<https://www.washington.edu/news/2014/11/14/top-canadian-limnology-award-goes-to-daniel-schindler-31-years-after-his-father-won-it/>)
- 4) Michael G. Scott Distinguished Lecturer, Humboldt State University, Oct. 9, 2013.
- 5) Institute of Ecosystems Distinguished Visiting Lecturer, University of Montana and Montana State University. Feb 2012.
- 6) Carl R. Sullivan Fishery Conservation Award from the American Fisheries Society to recognize the UW-Alaska Salmon Program, 2012.
- 7) Harriet Bullitt Endowed Chair in Conservation, University of Washington, 2011-2017.
- 8) H. Mason Keeler Professor of Aquatic and Fishery Sciences, University of Washington, 2008-2011.
- 9) Distinguished Research Award, College of Ocean and Fishery Sciences, University of Washington, June 2006
- 10) Distinguished Scholar, invited by Graduate Students. University of Minnesota-Duluth. March 2006
- 11) Invited Plenary Speaker, invited by Graduate Students, Ecological Integration Symposium, Texas A&M University, 2006.
- 12) Outstanding Reviewer Award, *Limnology & Oceanography*, 2005
- 13) Invited Participant, Beckman Frontiers of Science Symposium, US National Academy of Sciences, Beckman Center, Irvine California. November, 2003
- 14) Recipient of National Science Foundation, Doctoral Dissertation Improvement Grant. 1995.

7. University of Washington service activities

- 1) Chair, School Council – UW School of Aquatic and Fishery Sciences (2010-2018)
- 2) Alternate Member, College Council, UW-College of the Environment (2018-present)
- 3) Member, Steering Committee, EarthLab, UW-College of the Environment (2017-present)
- 4) Member, Promotion and Tenure Committee, UW-School of Aquatic and Fishery Sciences (2017-present)
- 5) Member, UW Royalty Research Fund Review Panel (2013-2015)
- 6) Member, Curriculum Committee, UW School of Aquatic and Fishery Sciences (2014-2015)

- 7) Member, Promotion and Tenure Committee, UW School of Aquatic and Fishery Sciences (2014-present, Acting Chair 2015)
- 8) Co-chair, UW - Freshwater Initiative (2012-present)
- 9) Co-Chair, Environment Institute, College of the Environment, UW (2009-2010)
- 10) Chair, Ten-year review of School of Oceanography (2009-2010)
- 11) Substitute for Director of SAFS on College of the Environment Executive Committee (2010-2011)
- 12) College Council – College of Ocean and Fishery Sciences (2004 – 2007, 2008-2009)
- 13) School Council – School of Aquatic and Fishery Sciences (2006-2010)
- 14) Substitute for the director of SAFS in inter-departmental discussion of the proposed College of the Environment. Winter 2008.
- 15) Seminar organizer – School of Aquatic and Fishery Sciences (Au2004, W2005, Sp2005, Sp2007, Sp 2008, Sp 2012, Sp 2013, Sp 2014)
- 16) Advisory Review Committee of the Deanship of the College of Ocean and Fishery Sciences (2006)
- 17) Member of Recruitment and Scholarship Committee, UW-SAFS, (2003-2004)
- 18) Seminar organizer – Department of Biology (W2000)
- 19) University of Washington, Royalty Research Fund, Reviewer

8. *Professional activities*

a. *Professional Organizations (Member)*

American Society for Limnology and Oceanography (ASLO)
 Ecological Society of America (ESA)
 American Fisheries Society (AFS)
 American Association for the Advancement of Science (AAAS)

b. *Editorial Responsibilities*

Subject Matter Editor for *Ecology* (June 2007 – present)
 Associate Editor for *Ecosystems* (July 2009 – present)
 Associate Editor *Climate Change Responses* (August 2013 – 2018)
 Associate and Subject-Matter Editor *FACETS* (2016-present)
 Guest Associate Editor for: *Proceedings of the National Academy of Sciences* (occasionally, 2007 – present)

c. *Select other professional activities*

- 30) Chair, Independent Peer Review Panel to Review Changes in Escapement Quality for Chinook salmon in the AYK region of Alaska. Arctic-Yukon-Kuskokwim Sustainable Salmon Initiative. (May 2018-present)
- 29) Chair, Canadian Foundation for Innovation, Expert Committee, Lake Observatories (January 2017, 2020)
- 28) Chair, Independent Peer Review Panel to Review Run Reconstruction and Spawner-Recruit Models for Chinook salmon in the Kuskokwim River. Arctic-Yukon-Kuskokwim Sustainable Salmon Initiative. (May 2016-present)
- 27) Chair, West Coast Protected Fish Species Science Program Review, NOAA Northwest Fisheries Science Center and Southwest Fisheries Science Center, (May 2015)
- 26) Scientific Advisory Committee, GRIL, Quebec Interuniversity Research Group in Limnology and Aquatic Environments, 2015-present.
- 25) Scientific Technical Committee - Arctic, Yukon, Kuskokwim Rivers-Sustainable Salmon Initiative. (2011-present)

- 24) Panel member, US-National Science Foundation, Coupled Natural Human Systems.
- 23) Chair, 10-year review of Editor-in-Chief of *Ecological Applications* – Ecological Society of America, June-Sept 2013.
- 24) Invited participant in think tank for implementing the Cohen Commission recommendations for recovery of Fraser River sockeye salmon. Simon Fraser University. March 25, 2013.
- 22) Chair – Chinook salmon in the Arctic, Yukon, Kuskokwim rivers of Alaska, for AYK-Sustainable Salmon Initiative (2011-2013)
- 21) Review panel, US-National Science Foundation, Coastal SEES program, Winter 2013.
- 20) Organizing committee member, Managing Species for Regulating the Carbon Cycle, Yale University Climate and Energy Institute, April 2012.
- 20) Panel member – Peer review panel report on Draft Klamath Dam Removal Overview Report for the Secretary of the Interior. (winter 2012).
- 19) Independent Scientific Panel Member to evaluate impacts of Chinook salmon fisheries on viability of southern resident killer whales, DFO-Canada and NOAA-USA (2011-2012)
- 18) Assessment of plankton community dynamics in Okanagan Lake for the British Columbia Ministry of the Environment (2009-2010)
- 17) Peer review of the scientific basis of the dissolved oxygen water quality objectives for the California Regional Water Quality Control Board (October 2009).
- 16) Chair, Aquatic Ecology Section of the Ecological Society of America. 2007-2009.
- 15) Steering Committee Member, National *Center for Ecological Analysis and Synthesis* workshop on effects of climate change on Pacific salmon. May 2006-May 2007.
- 14) Trustee - *The Nature Conservancy*, Washington Chapter. 2004 – 2008.
- 13) Vice-chair, Aquatic Ecology Section of the Ecological Society of America. 2005-2007.
- 13) Invited participant – workshop considering the importance of marine-derived nutrients in fisheries management. *The Nature Conservancy*, Alaska Chapter, Anchorage, Alaska, December 2006.
- 12) Advisor – *US National Park Service*, SW Alaska Division. 2004 - 2005.
- 11) Organizing Committee Member, American Society of Limnology and Oceanography, Annual Meeting, June 2006, Victoria, BC.
- 10) Panel Member - *Scientific Technical Committee for the Norton Sound Salmon Research and Restoration Fund* (Alaska Department of Fish and Game), 2003-2005.
- 9) Member - *Natural Heritage Advisory Council of Washington*, 2003 – 2007
- 8) Member - *Education and Human Resources Committee* of the *American Society of Limnology and Oceanography*. April 2002 – 2004.
- 7) Liaison between UW and City of Seattle, Cedar River Watershed, 2003-2004.
- 6) Workshop Participant: *US National Academy of Sciences* – The ecology and management of the Caspian Sea. Tehran, Iran, November 2002.
- 5) Panel Member: Developing a management and science program for Crescent Lake, Olympic National Park, WA. *US Geological Survey* and the *Olympic National Park*.
- 4) Member: *International Scientific Advisory Board* for the *Northwest Power Planning Council*. 2001 – 2002. Provides scientific recommendation for fish and wildlife recovery under the Endangered Species and the Northwest Power Act.
- 3) Workshop Participant: *National Center for Ecological Analysis and Synthesis* – Salmon Research Working Group – University of Santa Barbara. March 3-7, 2000.
- 2) Participant in workshop on assessing the ecosystem effects of pelagic fisheries for billfishes, tunas and sharks in the Pacific Ocean. University of Hawaii, Honolulu, HI. January 1999.
- 1) Member - *Lake Washington Technical Committee* 1997-2002

9. Bibliography (*Google Scholar: Citations = 19,488; h-index = 72, May 6, 2020*)

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- 2) McKinney, G.J., J.E. Seeb, C.E. Pascal, D.E. Schindler, S.E. Gilk-Baumer, and L.W. Seeb. Y-chromosome haplotypes drive variation in size and age at maturity in male Chinook salmon. (in review)
- 1) Gauthier, J., I. Gregory-Eaves, L. Bunting, P.R. Leavitt, T. Tran, L. Godbout, B.P. Finney, D.E. Schindler, G. Chen, G.W. Holtgrieve, M. Shapley, and D.T. Selbie. Evidence of anthropogenic changes driving the long-term ecological trajectory of a peri-urban lake, Cultus Lake, British Columbia: A multi-proxy paleolimnological study. (in review)

Other published contributions:

6. Schindler, D., and C. Cunningham. What if there's no salmon fishery? How COVID-19 could affect salmon populations. *National Fisherman*. April 14, 2020.
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THE EFFECTS OF SALMON FISHERIES ON SOUTHERN RESIDENT KILLER WHALES

FINAL REPORT OF THE INDEPENDENT SCIENCE PANEL

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Citation: **Hilborn, R., S.P. Cox, F.M.D. Gulland, D.G. Hankin, N.T. Hobbs, D.E. Schindler, and A.W. Trites. 2012. The Effects of Salmon Fisheries on Southern Resident Killer Whales: Final Report of the Independent Science Panel. Prepared with the assistance of D.R. Marmorek and A.W. Hall, ESSA Technologies Ltd., Vancouver, B.C. for National Marine Fisheries Service (Seattle, WA) and Fisheries and Oceans Canada (Vancouver, BC). xv + 61 pp. + Appendices.**

EXECUTIVE SUMMARY**Approach Used in the 2010 Biological Opinion**

The 2010 Biological Opinion (NMFS 2011a) and the presentations at the first two workshops developed a chain of logic for how Chinook salmon fisheries affect Southern Resident Killer Whales (SRKW). The logic can be described as follows:

1. SRKW depend upon Chinook salmon as a critical food resource. This is supported by summer diet information.
2. SRKW are occasionally in poor condition, which may indicate nutritional stress. Poor condition is supported by photogrammetry and observations of the “peanut-head” syndrome.
3. Individuals who have been identified as being in poor condition have a higher probability of dying than individuals who have not been so identified.
4. SRKW fecundity, death rates and rates of population increase have shown statistical correlations with some indices of Chinook salmon abundance.
5. Reducing Chinook salmon harvesting would increase the availability of Chinook salmon to SRKW.
6. Models using the coefficients of the statistical models (from item 4 above) suggest that there would be a slightly larger SRKW population on average if more Chinook salmon were available to SRKW.

The core of the analysis in the Biological Opinion is the statistical correlation between indices of Chinook salmon abundance and rates of increase in the SRKW population. The rest of the logic provides a mechanistic explanation for why that correlation could be causative.

The Conclusions of the Panel**Status of Southern Resident Killer Whales**

The SRKW population has on average been increasing slowly (about 0.71% per year) since the 1970s with alternating periods of increase and decline. Because of the small population size, much of the fluctuations may be the result of random events, but sustained periods of increase and decline, shared between both SRKW and NRKW (Northern Resident Killer Whales), suggest there is likely a common causal factor influencing their population dynamics. The two issues of concern about the status of SRKW are the low population size and the low rate of increase. Compared to NRKW the SRKW have a smaller population size, a slower growth rate, lower birth rates, and higher

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death rates. Historical population sizes were discussed in the 2010 Biological Opinion, and are also reviewed in Section 2.1 of this report.

Using the birth and death rates averaged over 1974 to 2011, the SRKW population should have grown at about 1% per year. The difference between this and the observed growth rate of 0.71% is due to the sex ratio—SRKW have had more surviving male births than surviving female births and thus an observed rate of increase that is lower than what would be expected if sex ratio of surviving births was 50:50.

The total population declined significantly for five years in the late 1990s and the largest pod (L pod) has declined further since 2000. There is serious concern about the L pod with only three surviving females producing surviving female offspring in recent years. The estimated rate of increase for the L pod is positive (see **Figure 2-1**), but this long term expectation assumes a stable age distribution (and the current age and sex distribution of the L pod is far from what one would expect on average). L pod has experienced low numbers of births due to the small number of adult females in prime breeding ages, but appears to have similar age-specific fecundity as females in the J and K pods.

Key Point:

The SRKW population has been observed to increase at an average rate of 0.71% per year, and would be expected to increase at about 1% per year in the long term if sex ratio at birth were 50:50.

The Panel believes that the existing delisting criterion of 2.3% growth rate is unlikely to be achieved given current circumstances or by reducing Chinook salmon fisheries, but given the estimated rates of increase, SRKW should eventually increase to a point where a reappraisal of their status would likely occur. It is difficult to estimate what the potential maximum population for SRKW may be, and NRKW, seals and sea lions all compete with SRKW for their food supply, which may limit the potential of SRKW to continue to increase in the long-term. The Biological Opinion discusses potential carrying capacities from a minimum of 140 animals to a maximum of 400. Demographic reconstruction showed that the largest known size was likely 96 animals in 1967 (Ford and Parsons 2012, slide 4), leading to the conclusion that the population size has not varied dramatically over the last 45 years. We would expect the rate of increase to decline as the population approaches the carrying capacity. The lower growth rate of SRKW compared to NRKW could be because the SRKW are closer to their carrying capacity.

Key Point:

The panel believes that the existing delisting criterion of 2.3% growth rate is unlikely to be achieved given current circumstances or by reducing Chinook salmon fisheries. But if the total abundance continues to increase, a point will be reached where a reappraisal of their status would be likely.

An alternative demographic analysis was presented to the Panel during Workshop 3 (Vélez-Espino et al. 2012) that reached conclusions that departed substantially from those presented in the first two workshops (discussed above). In particular the estimated rate of increase was slightly less than 1.0 (0.99) indicating that, on average, the population was expected to decline, although the uncertainty in this estimate means that positive growth rates cannot be ruled out. It is the conclusion of the Panel that the Vélez-Espino et al. analysis is preliminary. It is the Panel's understanding that the co-authors of this presentation had not yet reviewed it. The analyses presented in the earlier workshops by Ward had been more thoroughly reviewed. Major components of these analysis have undergone peer review and have been published (Ward et al. 2009, Ward et al. 2010). Thus, the Panel concludes that the most credible analysis of SRKW demographics at this point comes from the Ward presentations (Ward and Barre 2012, Ward et al. 2012).

SRKW Dependency on Chinook Salmon

Diet information from SRKW in the summer indicates a heavy reliance on Chinook salmon. As Chinook salmon abundance declines in the fall, the diet data show that chum salmon and other species become more important. There are little winter diet data, but the data that do exist also suggest the importance of Chinook salmon.

The age distribution of Chinook salmon consumed by SRKW does not match the predicted age distribution of Chinook salmon thought to be available to killer whales. Instead, SRKW consume greater proportions of the larger (older) fish (particularly the 4- and 5-year-olds) relative to the overall numbers of Chinook salmon present.

It seems somewhat illogical that SRKW would forgo feeding on other species of fish at times of low Chinook salmon abundance, and there are not enough data to determine if the percentage Chinook salmon in the diet is related to inter-annual variation in abundance of Chinook salmon. Other fish-eating killer whales in the North Pacific show a broader range of diet. However, the increase in the frequency of feeding on other species as summer ends and Chinook salmon availability declines does suggest that SRKW do switch to other species at times and places of low Chinook salmon abundance.

The Panel found the evidence for strong reliance on Chinook salmon in the summer convincing. However, given that the density of Chinook salmon in the summer as they migrate to the Fraser River is far higher than the density in the rest of the year when Chinook salmon are spread over a much larger area, it seems unlikely that the summer period would be the most critical period where Chinook salmon abundance affected SRKW vital rates.

Key Point:

The evidence for strong reliance on Chinook salmon in the summer is convincing, but it is also clear that SRKW will switch to alternative, more abundant chum salmon when Chinook of suitable size and quality are not readily available in the fall.

Poor Condition and Possible Nutritional Stress

Some SRKW have been seen in poor condition (which can be caused by nutritional stress or other factors) and animals in poor condition have a higher probability of dying. The strongest suggestion of poor condition is the photographic evidence from Durban et al. (2009) that documented 13 SRKW in poor condition over the period 1994 through 2008—of which all but two of these individuals subsequently died. Poor condition and nutritional stress could contribute to increased mortality or reduced fecundity of SRKW through a variety of mechanisms (i.e., direct starvation, increased susceptibility to trauma due to increased movements to forage, decreased resistance to infectious disease, mobilization of lipophilic toxic chemicals), as well as to decreased recruitment through changes in calving interval and calf survival. There are insufficient data to relate the incidence of poor condition to nutritional stress caused by low Chinook salmon abundance or other causative factors. These data serve primarily to support the assertion that poor condition, which is clearly linked to increased risk of mortality, and by implication to fecundity, may reflect nutritional stress.

The Panel believes the photographic evidence is convincing that poor condition (and *possibly* nutritional stress) is an issue of concern for SRKW. However, not all members of the Panel were convinced that poor condition was *necessarily* an indicator of nutritional stress (due to low availability of prey) as compared to some other factor (disease, organ malfunction) that might lead to reduced or less successful feeding and thereby generate "poor condition". Unless a large fraction of the population experienced poor condition in a particular year, and there was ancillary information suggesting a shortage of prey in that same year, malnutrition remains only one of several possible causes of poor condition.

Presentations on fecal hormone levels argued that the decline in T3 values through spring and summer indicated nutritional stress during this period. This change could be explained by changes in photoperiod, as well as by individual differences in nutritional status, age, sex, reproductive status, stress, and PCB exposure of individuals sampled. Unfortunately, the lack of fecal hormone data in winter months due to logistical difficulties associated with sample collection limits the current utility of the available fecal hormone data to assess the nutritional status of the SRKW.

Key Point:

Photographic evidence supports the assertion that poor condition, which is linked to mortality, and by implication to fecundity, may reflect nutritional stress. However, unless a large fraction of the population experienced poor condition in a particular year, and there was ancillary information suggesting a shortage of prey in that same year, malnutrition remains only one of several possible causes of poor condition.

Fisheries and Prey Availability**Trends in Chinook salmon abundance**

Contemporary abundances of Chinook salmon in the Pacific Northwest and California have been greatly reduced from historic abundances and many Evolutionarily Significant Units (ESUs) of Chinook salmon are listed as threatened or endangered under the US Endangered Species Act. Many British Columbia stocks of Chinook salmon have also been identified as stocks of conservation concern. Declines in abundance of spring-run fish have been particularly evident in California's Central Valley, in the Columbia River (interior spring Chinook salmon) and in Puget Sound. Associated with the declines in abundance have also been shifts in age structure of many populations toward younger ages and smaller adults.

Comparing averages for 2001-2010 with those for 1979-1988 and considering stocks of likely importance to the SRKW, (1) Fraser Early Chinook salmon total abundance (terminal¹ run + fishery impacts) has increased by about 36%, and terminal run size has increased by more than 100%; (2) West Coast Vancouver Island aggregate total abundance has decreased by 35%, but terminal run sizes have increased by about 19%; (3) Fraser Late Chinook salmon total abundance has decreased by about 51%, but terminal run size has increased by about 38%; and (4) Puget Sound total abundance has decreased by about 38%, but terminal run size has not changed. Coast-wide, there has been an approximately 16% decrease in total Chinook salmon abundance over this period, but a concurrent 37% increase in ocean escapement to terminal areas. Substantial reduction in ocean fishing has resulted in more Chinook salmon being available to SRKW during the summer when they feed on homeward bound fish, despite a slight decrease in total Chinook salmon abundance.

Spatial and temporal overlap between SRKW and Chinook salmon stocks

SRKW are found almost exclusively in the Salish Sea and in coastal waters near the entrance to the Strait of Juan de Fuca during the July–September period. During the April–June period, only about 32% of SRKW sightings have been in the Salish Sea with remaining sightings primarily in coastal waters off northern Oregon and Washington and outside waters off Vancouver Island. During winter months, SRKW are sometimes distributed off of central California and seem to be found more frequently off the Washington coast.

¹ terminal fisheries are those that take place on mature fish as the return, either in freshwater or in saltwater in the vicinity of their natal streams.

Available data are inadequate to allow assessment of winter (January–March) distribution patterns of both Chinook salmon and SRKW, so it is not possible to reliably assess the possible degree of overlap of SRKW and Chinook salmon during this period. However, SRKW tissue carbon and nitrogen stable isotope and contaminant fingerprint analyses are consistent with a SRKW diet comprised of Chinook salmon from a wide range of sources well outside the narrowly defined Puget Sound/Fraser River area.

Would reducing harvest increase Chinook salmon availability?

Recent analyses presented at the workshops explored whether reductions in Chinook salmon harvest would increase food for SRKW and thus SRKW population rates of increase. These analyses assume that a certain number of Chinook salmon foregone from the harvest will result in an equivalent increase in abundance of Chinook salmon for SRKW. They assume that closing all ocean fisheries will directly result in short-term increases in the abundance of Chinook salmon that are available to SRKW.

Eliminating ocean fisheries and managing freshwater fisheries for maximum recruitment would result in an additional long-term increase in the total Chinook salmon population compared to the present due to the elimination of ocean interception of immature salmon prior to maturity and higher escapements resulting from the reduction in terminal fisheries. For a given stock, this benefit would depend on the current age-specific ocean fishery exploitation rates and the stock-specific maturation schedule. However, the long-term benefits appear to be rather small. Assuming that current escapements and exploitation rates are those that maximize sustainable yield means that Chinook salmon escapements are currently close to levels that produce maximum total Chinook salmon recruitment. This is the assumption of the management agencies, and the Panel was not in a position to review the underlying analysis of the management agencies. Hatchery stocks are generally at full production and not limited by escapements, so increase in escapements would not result in increased hatchery production. Efforts to rebuild Chinook salmon runs depend primarily on restoring the productivity and carrying capacity of freshwater spawning, rearing and migratory habitats. The other potential for substantially higher Chinook salmon returns is a change in ocean conditions which might return ocean survival to the higher rates seen prior to the 1980s. This is beyond management control, but there is some evidence that ocean survival rates of Chinook salmon have increased in recent years.

Key Point:

The maximum long-term increases in abundance of Chinook salmon that might theoretically be available to SRKW would be achieved by eliminating all ocean fishing (typically at least 20% increase in ocean abundance of age-4 and age-5 hatchery and wild fish due to elimination of ocean fishery interception of immature fish) and by maximizing recruitment through manipulation of freshwater exploitation rates to maximize recruitment (6-9% increase in recruitments of wild fish; no impact on hatchery fish).

The best potential for increased Chinook salmon abundance is restoration of freshwater habitat, reducing downstream migration mortality and a change in ocean conditions.

Does reduced Chinook salmon catch result in equivalent increase in Chinook salmon for SRKW?

There are several reasons why reductions in ocean catch of Chinook salmon do not equate to an equivalent increase in availability of Chinook salmon to SRKW. First and foremost, there are a range of other predators on Chinook salmon, especially NRKW, harbor seals and sea lions that may eat some of the foregone Chinook salmon before or at the same time that the SRKW have access to them. The actual increase in food availability to SRKW may be considerably less than the foregone harvest.

Second, the foregone harvest would likely not consist exclusively of Chinook salmon stocks that are important to SRKW. Most Chinook salmon harvesting takes place on a mix of stocks, and some foregone harvest would almost certainly be fish not important or critical to SRKW.

Third, if Chinook abundance in the summer is critical, then the key Chinook salmon in summer are mature fish. Yet many of the Chinook salmon fisheries harvest a mix of immature and mature fish. While the foregone immature fish would ultimately become mature if they survived, not all would survive and thus not all foregone harvest would result in mature fish. The abundance of immature mature fish in summer available to SRKW would not increase equally with foregone immature Chinook salmon harvest because of the other sources of mortality that would occur between the time of foregone catch and availability in the summer to SRKW.

Finally, the currently low ocean harvest rates on Chinook salmon (on the order of 20% on average) means that there is limited opportunity for reductions in Chinook salmon harvesting to increase the abundance of Chinook salmon.

The Panel sees many potential reasons why all foregone Chinook salmon catch would not be available to SRKW, and is therefore skeptical that reduced Chinook salmon harvesting would have a large impact on the abundance of Chinook salmon available to SRKW.

Key Point:

The panel sees many potential reasons why not all foregone Chinook salmon catch would be available to SRKW, and is therefore skeptical that reduced Chinook salmon harvesting would have a large impact on the abundance of Chinook salmon available to SRKW.

Projected Future Status and Recovery**Statistical correlation between Chinook salmon abundance and rates of increase in SRKW**

Several analyses performed by both NOAA and DFO have shown correlations between Chinook abundance and the rate of increase for SRKW. The presentations at Workshop 2 by Eric Ward and co-authors used the Kope-Parken index of salmon abundance and showed significant correlation between the Chinook salmon abundance index and SRKW survival, and a weak indication of some impact on fecundity. This analysis is the core of the evidence that changing Chinook salmon abundance affects SRKW demographic parameters. The statistical analysis performed used modern methods and has been very thorough. The Panel considers the methods used to evaluate the relationship between salmon abundance and SRKW fecundity, survival, and population growth rates scientifically reasonable and state-of-the-art.

Although there is a reasonable body of scientific evidence showing that Chinook salmon are important prey for SRKW, there is a limited range of specific observational evidence and no possibility of experimental evidence linking Chinook salmon abundance to SRKW population growth. Because SRKW growth and salmon abundance data are observations of uncontrolled events obtained from an unknown sampling design, there is a high risk of incorrectly assigning causes to correlations and making weak inferences.

A major concern is the choice of indices of Chinook salmon abundance. The Panel believes that an index that reflects overall Chinook salmon abundance would be the most likely to reflect food available to SRKW over both summer and winter.

The fact that density dependence was stronger in the NRKW population than in the SRKW population (Ward et al. 2012a, slide 59) suggests that the northern population should experience stronger bottom-up limitations as the population grows, a prediction that is contrary to observations. All of these difficulties of interpretation cast doubt on a simple, causal interpretation of the positive correlation between salmon abundance and SRKW vital rates. However, the Panel must also point out that the relatively narrow range of density during the period of analysis may mean that there was insufficient statistical sensitivity to detect effects of density. The Panel believes the NOAA and DFO scientists have done an excellent job of their statistical analysis, but in the end believe considerable caution is warranted in interpreting the results as confirming a linear causative relationship between Chinook salmon abundance and SRKW survival.

Key Point:

The statistical analysis by NOAA and DFO scientists are excellent, but the Panel believes considerable caution is warranted in interpreting the correlative results as confirming a linear causal relationship between Chinook salmon abundance and SRKW vital rates.

Estimating the Impact of Reducing Chinook Salmon Fisheries on SRKW

In the original Biological Opinion on the Puget Sound Chinook Harvest Management Plan, NOAA Fisheries devised and evaluated alternative fishery regimes to assess their relative impact on future status and recovery of SRKW (NOAA/DFO letter to Panel, Aug. 22, 2012). Over the course of three workshops, the alternative fishery regimes have essentially been reduced to two: (1) maintain status quo with ocean fishery exploitation rates on the order of 20%; and (2) close all ocean fisheries. Such a simplification is probably warranted in this case given what appears to be a revised understanding of interactions between fisheries and SRKW. In particular, it seems to be a gross extrapolation to implicate any particular fishery, including those during the peak period of Chinook salmon abundance in summer, in affecting SRKW population growth rate. Instead, a more plausible working hypothesis is that highly mobile SRKW (and NRKW) respond to larger spatial scale changes in Chinook salmon abundance than can be appreciably affected by any specific Chinook salmon fishery.

The evidence seems reasonably strong that vital rates of SRKW are, to some degree, ultimately affected by broad-scale changes in their primary Chinook salmon prey. However, even if there is a causal mechanism, the Panel's opinion is also that such a mechanism is probably not a simple linear cause-and-effect one for a variety of reasons. For example, if Chinook salmon abundance is causally related to SRKW mortality and fecundity, then it also seems likely that SRKW (and other predators) can cause changes in Chinook salmon mortality. Such feedbacks imply non-linear density dependence in SRKW growth rate (e.g., a large region of Chinook salmon abundance over which growth response is small, but a small region where growth response is large). The logistic regression models and supporting auxiliary evidence reflect only a narrow range of abundance for both SRKW predators and their Chinook salmon prey, which increases the risk of poorly capturing these relationships. Thus, the Panel's overall view is that the predator-prey system involving Chinook salmon, SRKW, NRKW, and some pinnipeds is only partially described by correlations between Chinook salmon and SRKW. Therefore, any predictions about impacts of changing fisheries may not be robust to changes in the status of other Chinook salmon predators, or even to changes in Chinook salmon abundance.

Key Point:

The Panel is not confident that understanding of the interaction between Chinook salmon fisheries, other predators and SRKW vital rates, is sufficient to expect the model predictions of increased SRKWs to be accurate.

The Panel expects the model predictions to overestimate the impact of reductions in Chinook salmon catch on SRKW.

Mechanisms for Chinook Salmon Abundance Impacting Killer Whale Vital Rates

Much of the work done by NOAA and DFO, and contained in the Biological Opinion, relates to mechanisms that support the statistical correlation between indices of Chinook salmon abundance and vital rates of SRKW. The basic mechanism is that SRKW are on some occasions food limited, leading to poor condition and lower survival and fecundity, and that Chinook salmon are a highly important part of their food supply. NOAA and DFO have documented that some killer whales are in poor condition, that those in poor condition have lower survival, and that Chinook salmon are an important part of SRKW diet. The mechanistic data developed so far provide some support for causation. Support for causation would be weakened if there were no evidence for poor condition (possibly due to nutritional stress) or if Chinook salmon were not an important part of SRKW diet.

This mechanistic approach does not provide a quantitative method to evaluate the benefits of reducing Chinook salmon harvesting. What is needed is documentation of the relationship between Chinook salmon abundance and the number of animals that are in poor condition. This could provide strong evidence that periods of low Chinook salmon abundance lead to poorer condition, more nutritional stress and lower survival rates. The major limitation to the mechanistic approach at present is that very little information on condition is currently available to provide scientific or management guidance. Similarly there is so little information on winter diet that the mechanistic approach must presently remain merely supportive of causation.

Conclusions

The Panel believes that the estimated benefits of reducing Chinook salmon harvest in NOAA's recent analyses provide a maximum estimate of the benefits to SRKW—and that the realized benefits would likely be lower and insufficient to increase growth rates to a level that meets existing SRKW delisting criteria in the foreseeable future.

The Panel concludes that there is good evidence that Chinook salmon are a very important part of the diet of SRKW and that there is good evidence, collected since 1994, that some SRKW have been in poor condition and poor condition is associated with higher mortality rates. There is a statistical correlation between SRKW survival rates and some indices of Chinook salmon abundance. Based on those correlations, increases in Chinook salmon abundance would lead to higher survival rates, and therefore higher population growth rates of SRKW. However, the effect is not linear as improvements in SRKW survival diminish at Chinook salmon abundance levels beyond the historical average. Using the statistical correlations, consistently positive SRKW growth rates can

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occur by avoiding extremely low Chinook salmon abundance levels observed in the 1970-80s and late-1990s. Elimination of ocean fisheries for Chinook salmon would impact Chinook salmon abundance far less than the variations that have been seen since the 1970s.

The Panel cautions against overreliance on the correlative studies, and notes that the level of correlation is highly dependent on the choice of Chinook salmon abundance indicators. The impact of reduced Chinook salmon harvest on future availability of Chinook salmon to SRKW is not clear.

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1.0 INTRODUCTION

This report is the final report of the Independent Science Panel of the Bilateral Scientific Workshop Process to Evaluate the Effects of Salmon Fisheries on Southern Resident Killer Whales. This section provides a brief overview of the background context, workshop process, the role of the Independent Science Panel, and an introduction to the structure of the present report.

1.1 Context

Southern Resident Killer Whales (SRKW; *Orcinus orca*) are listed as an endangered species under both the Endangered Species Act (ESA) in the US and the Species at Risk Act (SARA) in Canada. The National Marine Fisheries Service (NOAA Fisheries) and Fisheries and Oceans Canada (DFO) have developed and adopted recovery plans for SRKW as required by their respective national statutes. One of the potential threats to the recovery of SRKW may be a reduction in salmon prey available to SRKW due to salmon fisheries. During 2011-2012, NOAA Fisheries and DFO commissioned a series of three scientific workshops to rigorously explore the evidence available to answer the key question:

To what extent are salmon fisheries affecting recovery of SRKW by reducing the abundance of their available prey, and what are the consequences to their survival and recovery?

As part of the workshop process, the NOAA and DFO Steering Committee appointed an expert science panel ("the Panel") to provide an independent review of the evidence available and advice on future research. The scientists from the national, state and tribal fisheries agencies, members of the Panel and other participants in the workshops examined existing research as well as completely new research directed by the outcomes of the first two workshops.

1.2 Workshop Process

The detailed design of the workshop process and various outputs of this process, including workshop presentations, background literature, new materials developed for the workshops, preliminary responses from the Panel, and feedback from other participants are all available elsewhere. In this report, the Panel wishes to avoid repeating information that is readily available in other documents. Instead, a brief summary is provided below of other documents, reports and materials associated with the overall workshop process. The following materials are currently all available at <http://www.nwr.noaa.gov/Marine-Mammals/Whales-Dolphins-Porpoise/Killer-Whales/ESA-Status/KW-Chnk.cfm>.

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1. **Process Description** – describes the overall workshop process; the role of the Panel, the Science Panel Chair, and the Science Facilitator; the flow of tasks through the entire process; and the contextual background (both scientific and regulatory) to the key question.
2. **Process Diagram** – outlines the timeline associated with the major tasks and stages of the overall workshop process.
3. **Reading List** – breaks the overall question into the original topics used by the Panel to organize their assessment, provides a contextual description of each topic, poses key questions for each topic, and provides an extensive list of relevant background literature.
4. **Background Literature** – a comprehensive library of relevant background literature compiled by the Steering Committee prior to the Workshop 1 for participants and panel members to review.
5. **Workshop Agendas** – lists all the speakers and presentations for each of the three workshops.
6. **Workshop Presentations** – the final presentations delivered by each of the speakers at each of the three workshops.
7. **Workshop Audio Files** – audio recordings of the entire proceedings of each workshop.
8. **Response Papers** – short papers prepared by NOAA and DFO scientists in response to requests from the Panel for additional information on particular topics. These response papers were prepared in place of presentations on these topics at Workshop 2.
9. **Additional Workshop Materials** – additional materials provided by presenters and participants, including supplementary papers or data sets, short papers on additional research not presented, and official institutional statements.
10. **NOAA and DFO Questions & Answers** – provides responses from NOAA and DFO scientists to short-term information / analysis requests that the Panel provided to the Steering Committee shortly after Workshops 1 and 2.
11. **Workshop 1 Proceedings** – includes questions and discussion from Workshop 1 integrated into a compilation of all of the responses (feedback, comments, recommendations, etc.) received from participants following Workshop 1.
12. **Participant Responses to Workshop 2** – written comments, feedback and additional analyses submitted by participants to the Panel in response to Workshop 2.
13. **Science Panel “Reflections” Document** – the preliminary report of the Panel following Workshop 1, including initial responses and recommendations for work to be done prior to Workshop 2. The Panel based its responses on the evidence available prior to the workshop, the presentations and discussion at the workshop, the information available immediately following the workshop, and the feedback submitted by other participants.
14. **Draft Report of the Independent Science Panel** – the May 3, 2012 draft report, completed subsequent to Workshop 2. This draft report was available for public comment for a period of six weeks.
15. **Public Comments on the Draft Report** – the comments and responses submitted during the public review period. Comments were received from individuals and organizations.

1.3 The Independent Science Panel

The Independent Science Panel (“the Panel”) consists of seven senior scientists from five US and Canadian universities and one non-university research institution. These scientists were chosen to be members of the Panel according to their relevant expertise in salmon fisheries, killer whales and predator-prey dynamics, and their ability to constructively and objectively collaborate to fulfill the purposes of the workshop process. The Panel comprises the following members:

Dr. Ray Hilborn (Chair)

School of Aquatic and Fishery Science, University of Washington, Seattle, WA

Dr. Sean Cox

School of Resource and Environmental Management, Simon Fraser University, Burnaby, BC

Dr. Frances Gulland

Marine Mammal Center, Sausalito, CA

Dr. David Hankin

Department of Fisheries Biology, Humboldt State University, Arcata, CA

Dr. Tom Hobbs

Natural Resource Ecology Lab, Colorado State University, Fort Collins, CO

Dr. Daniel Schindler

School of Aquatic and Fishery Science, University of Washington, Seattle, WA

Dr. Andrew Trites

Marine Mammal Research Unit, University of British Columbia, Vancouver, BC

The principal role of the Panel is to critically evaluate the scientific evidence available and the approach by which that evidence is being used to answer the central question. The Panel attended all of the workshops, questioning the presenters and participating in discussions. In their first report (Hilborn et al., 2011), delivered in November 2011, the Panel provided initial, preliminary responses based on the evidence available prior to Workshop 1, the proceedings of Workshop 1, and the comments and feedback of other participants. The Panel then revised these responses while working on its draft final report (Hilborn et al., 2012), in light of new information and analyses presented at Workshop 2 and additional input from participants.

The Panel then revised its draft report in consideration of the comments received during its public review period, the agency-level comments provided by NOAA and DFO in response to the draft report, and the information presented at the third workshop. Workshop 3 was organized around the topics most frequently or critically addressed in the public comments as well as outstanding questions from the Panel itself. Its focus was to provide new information or clarify existing information where such information could potentially alter the conclusions of the Panel. As the Panel refined its final report, it considered the comments and criticisms received during the public review period, as well as the new, clarified, or re-emphasized information presented at Workshop 3. The ultimate goal of the Panel has been to examine current methods of addressing the central question and provide guidance for future research to reduce critical uncertainties.

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The responsibility of the Panel explicitly excludes addressing management issues or making management recommendations. The responsibility of the Panel only covers the critical examination of scientific issues. The Process Description thoroughly describes the full role of the Panel.

1.4 Report Overview

The Executive Summary provides an integrated discussion of the most critical themes identified by the Panel and the recommendations that the Panel considered to be of the highest priority across all of the broad topic areas. The Executive Summary is intentionally longer and more thorough than is typical for report of this size. This thorough synthesis of the responses and recommendations of the Panel is not repeated in the main body of the report.

Sections 2.0 to 5.0 provide an examination of each of four broad topic areas in depth. These topic areas represent a consolidation of the nine topics originally identified by NOAA and DFO and addressed in the Panel's preliminary report subsequent to Workshop 1. The Panel felt that considerable overlap existed among the original topics both in terms of the questions being asked and the evidence available to answer those questions, and that a consolidation of these topics would allow the Panel to address the total suite of questions in a more effective manner. **Table 1-1** illustrates how those original topics were consolidated for the purposes of the Panel's final report. **Appendix A** provides a complete listing of the original questions posed to the Panel within each topic. Each of these sections serves four broad functions: 1) providing a contextual introduction to the particular topic, including relevant background information; 2) reiterating or summarizing the key questions asked of the Panel across the original topics consolidated into each section; 3) reporting the Panel's assessment and conclusions in response to those questions; and, 4) providing recommendations, where appropriate, for future research and analysis to reduce key uncertainties and improve the level of scientific understanding.

Table 1-1. Consolidation of original topics into the sections of the current report.

Report section	Section title	Topics as originally defined by the NOAA and DFO Steering Committee and addressed in this report
2.0	Status and Growth Rates of Killer Whales	<ul style="list-style-type: none"> • Status of Killer Whales
3.0	Feeding Habits and Energetic Needs of Killer Whales	<ul style="list-style-type: none"> • Feeding Habits and of Killer Whales • Chinook salmon Needs of Southern Resident Killer Whales • Ratio of Chinook salmon Food Energy Available Compared to Chinook salmon Food Energy Needed by Southern Residents with (and without) Fishing
4.0	Fisheries and Prey Availability	<ul style="list-style-type: none"> • Fisheries that May Affect Prey Availability • Reduction in Chinook salmon Abundance from Fisheries
5.0	Projected Future Status and Recovery	<ul style="list-style-type: none"> • Relationship between Chinook salmon Abundance and Killer Whale Population Dynamics • Change in Killer Whale Population Growth Rates Annually, Abundance over Time and Species Survival and Recovery

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The views, conclusions and recommendations of the Panel reported in this document have been informed by multiple sources of evidence within the workshop process (in roughly chronological order):

- literature reviewed prior to Workshop 1
- presentations and discussion at Workshop 1
- responses from NOAA and DFO scientists to short-term requests from the Panel immediately following Workshop 1
- feedback and comments submitted by participants in response to Workshop 1
- feedback from NOAA and DFO scientists on the Panel's preliminary responses
- presentations and discussion at Workshop 2
- response papers prepared for Workshop 2
- additional information and materials provided by participants for Workshop 2
- responses from NOAA and DFO scientists to short-term requests from the Panel immediately following Workshop 2
- direct discussions with NOAA and DFO scientists to clarify methodological questions
- feedback and comments submitted by participants in response to Workshop 2
- feedback and comments submitted by individuals and organizations in response to the Panel's draft final report during the period of public review
- agency-level comments from NOAA and DFO in response to the Panel's draft final report
- presentations and discussion at Workshop 3
- presentations, discussions and written handouts as part of the "correlation vs. causation panel" at Workshop 3
- additional information and discussion provided by workshop participants on the details of their analyses and methodologies, including John Carlile, John Ford, Mike Ford, Robert Kope, Larrie LaVoy, Chuck Parken, Antonio Vélez-Espino, Eric Ward, and many others.

2.0 STATUS AND GROWTH RATES OF KILLER WHALES

2.1 Context

Data on the abundance and demography of killer whales are unusually detailed as a result of the ability to recognize individuals by photographing their dorsal fins and adjacent markings. Photo identification allows every individual in the population to be observed over time, providing strong data for estimation of population size and vital rates. However, there are limitations to the demographic data. There is very little information on neonatal survival. Causes of deaths are largely unknown.

The abundance of SRKW fluctuated between 67 and 95 individuals during 1974 to 2011 (see **Figure 2-2**). Intervals of population increase alternated with periods of decline, but the duration of intervals of positive growth substantially exceeded those when growth was negative. During 1974 to 2011, the population has been increasing slowly, from 67 individuals in 1974 to 87 individuals in 2011, at a realized growth rate of 0.71% per year (see **Box 2-1**).

Box 2-1. Calculating growth rates.

It is important to distinguish the observed population changes (and thus the realized growth rate) from the expected growth rate λ .

The **realized growth rate** is simply the exponential rate of increase which, when applied for a series of years to an observed population abundance at the start of a time period, leads to the observed population abundance at the end of the time period.

$$RGR = \left(\frac{N_{t_2}}{N_{t_1}} \right)^{[1/(t_2-t_1)]}$$

Where:

RGR = Realized annual growth rate

t_1 = Start of time period over which RGR is estimated (e.g., 1974)

t_2 = End of time period over which RGR is estimated (e.g., 2011)

N_{t_1} = Population abundance at time t_1 (e.g., 67)

N_{t_2} = Population abundance at time t_2 (e.g., 87)

Converting RGR into an annual percentage growth rate is done as $(RGR-1)*100$

Lambda (λ) is the growth rate that would be expected in the long term given a stable age distribution and a 50:50 sex ratio at first sighting. The observed population growth rate may be lower or higher than λ because of the interaction of sex ratio, random stochastic events and age structure (Caswell 1988).

In contrast to SRKW, NRKW have increased more rapidly over the same time interval, from 120 animals in 1975 to more than 260 currently. The trajectory of growth has been, for the most part, steadily positive over the last three decades. Increases in abundance were interrupted only briefly during the late 1990s and early 2000 when the population declined at a rate of one percent annually, a downturn that coincided with steeper declines in the abundance of SRKW.

The history of predominantly positive growth rates in SRKW would promote confidence about the future persistence of the population if the population were large. However, the relatively small size of the population raises concerns about its viability as a result of environmental and demographic effects exposing the population to risks of extinction. A key point, occasionally overlooked by participants in the first two workshops, is that the SRKW population is *not* declining. The population appears to be growing with some variation that can be attributed to expected annual fluctuations in vital rates characteristic of populations of vertebrates. Concerns about its future arise primarily from the current and recent size of the population and the potential impacts of future, unforeseen events on a population that lacks the resilience created by higher abundance. Moreover, there is serious concern about the future of the L pod, where demographic stochasticity has caused an imbalanced sex ratio such that there are more adult males than females, leading to a long period of declining abundance.

2.2 Key Questions

Understanding the current status of the SRKW population is a necessary starting point for any discussion of actions needed to improve its status. The Panel was asked to examine current knowledge of population size, growth rates, and demography of SRKW relative to NRKW (Northern Resident Killer Whales), to assess current trends relative to historical trends in abundance and to evaluate understanding of the current status of the population relative to recovery goals.

2.3 Responses to Key Questions

Population Growth Rate

Observations of known individuals over an extended period of time allow estimation of vital rates of populations that are more accurate than those based on data lacking individual histories. Thus, the database used in the demographic analysis is a notable strength. The analyses conducted to infer population trends were state-of-the-art in their statistical and mathematical sophistication. The Panel finds little fault in the data or in their implementation in models of historic population dynamics.

Analysis of the long-term population growth rate (hereafter, λ) of the population of SRKW from data obtained during 1970-2010 revealed reasonably strong evidence that the population is increasing (Ward and Barre 2012, Ward et al. 2012a). There were large differences in λ among pods, with J and K pods showing the strongest evidence of growth. The posterior distribution of λ for the L pod revealed that values for $\lambda < 1$ cannot be ruled out (**Figure 2-1**).

It is important to reconcile the mostly positive posterior distribution of λ for the L pod with the observation of declines in their numbers since the early 1990s (**Figure 2-2**). This can be explained by the way λ was calculated for the L pod. Because there were no significant differences in age-specific fecundities, these were pooled for use in the λ analysis for individual pods. Because age-specific survivals tended to be lower in the L pod than in the other two pods, the λ analysis applied different survival (i.e., lower) probabilities for the L pod. Thus, the difference in stage-specific survival rates would be responsible for the downward shift in distributions of λ for L pod compared to J and K pods, but the assumption that L pod age-specific fecundities were the same as for J and K pods would move the distribution of λ for L pod upward toward that for J and K pods.

The mean value of λ across J, K, and L pods was less than the recovery goal of 1.023. However, the distribution of possible λ values includes values that *exceeded* recovery goals, as well as values of λ less than one. The key result here is the uncertainty about the expected long-term population's growth rate. Analysis by Eric Ward following Workshop 3 indicated that this conclusion was not sensitive to the starting point of the time interval over which the growth rate was calculated.

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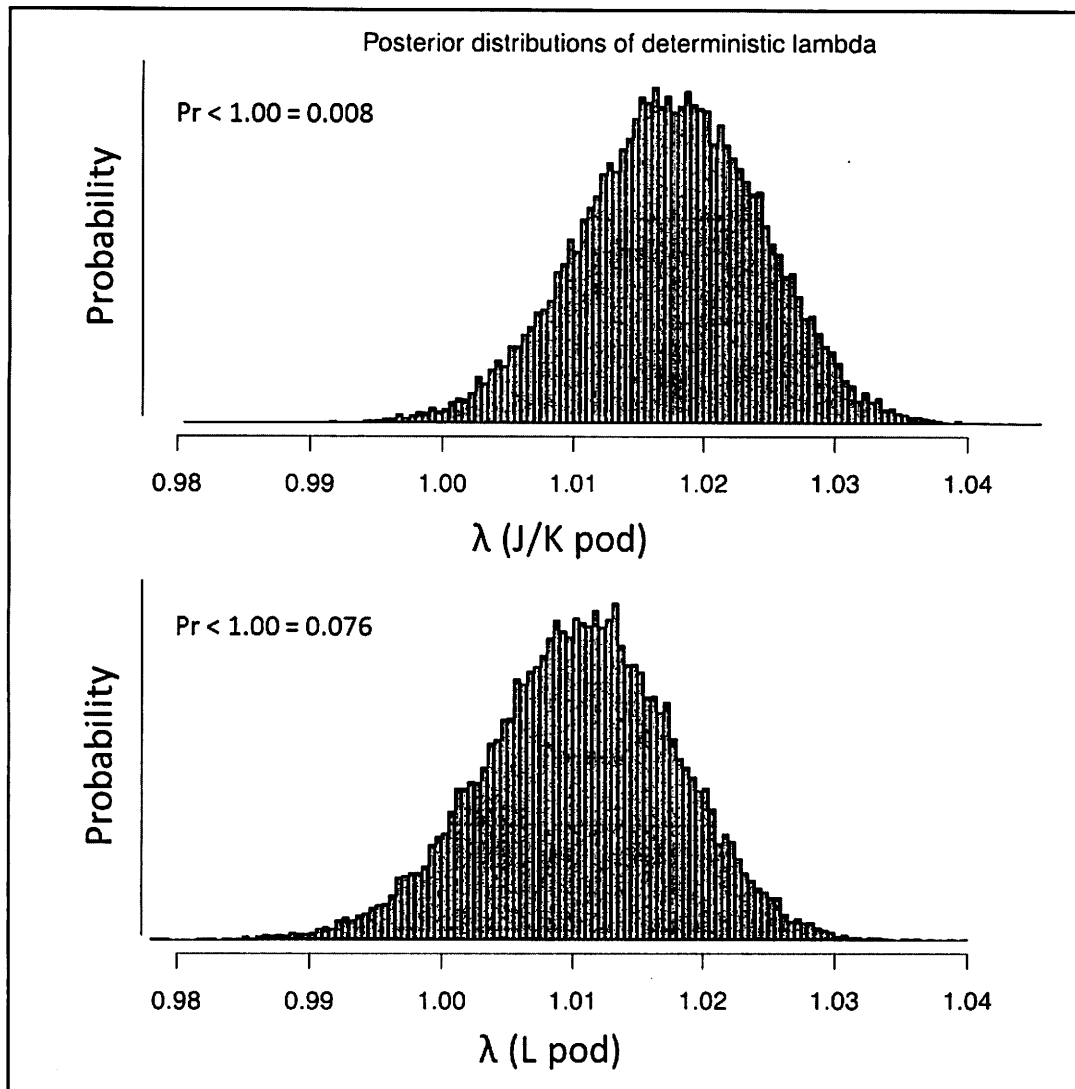


Figure 2-1. Estimates of the posterior distribution of population growth rate. “Pr < 1.00” is the probability that $\lambda < 1.00$ (the red area under the probability distribution), or the probability that the population may be experiencing a long term population decline. Source: Ward et al. 2012a.

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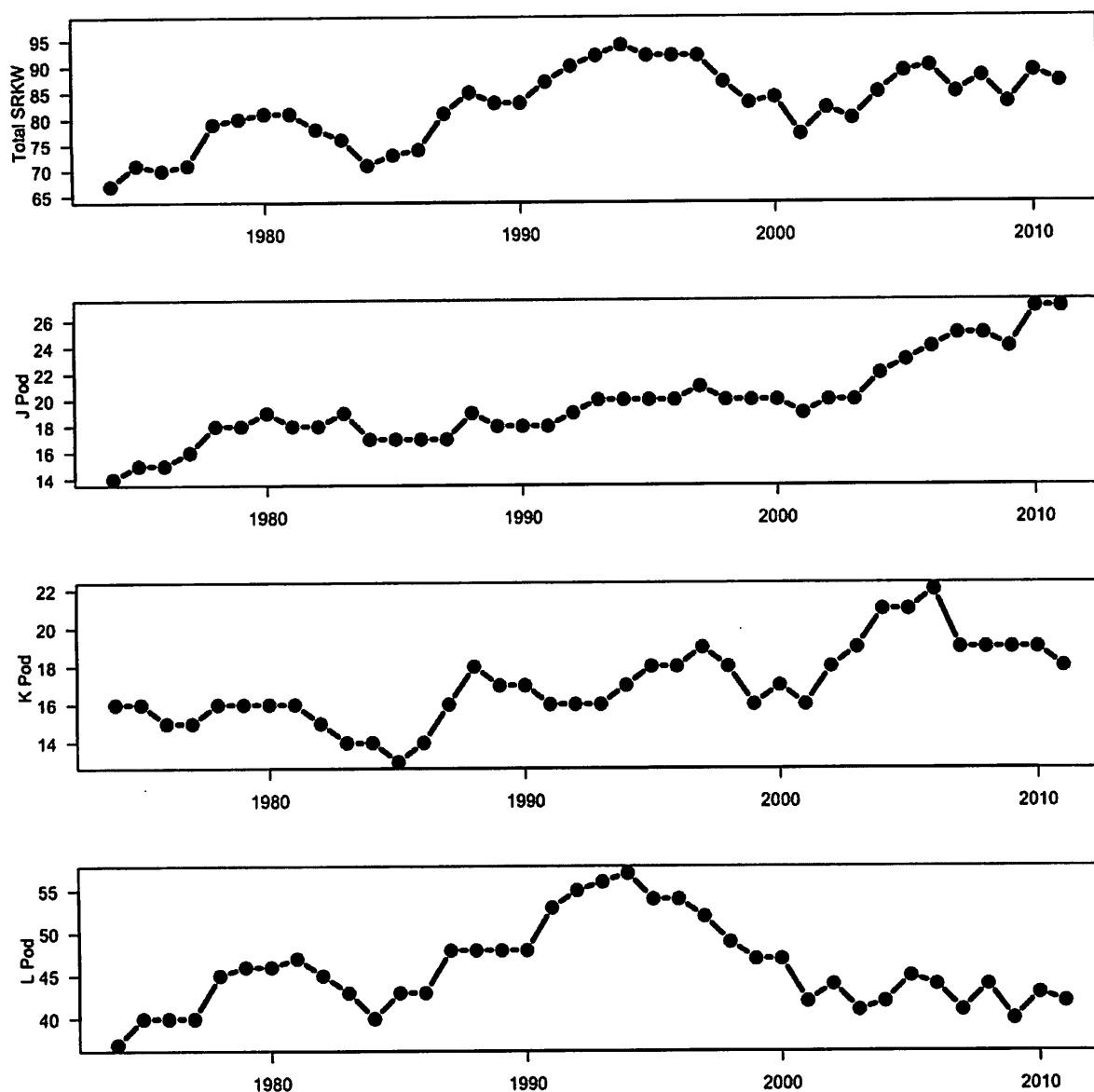


Figure 2-2. Observations of total population size for the entire SRKW population (top panel) and for each pod (bottom three panels). Source: Eric Ward email to the Panel, Sept. 20, 2012; updated Nov. 27, 2012)

The evidence that recovery goals may be met in the long-term results in part from the assumptions required by the analysis of λ . The λ analysis only applies to time scales of decades and applies only to populations at long-term equilibrium for sex and age composition (but not for abundance). What this means is that the estimate for λ depends on a mix of sexes and ages that would be expected on average over many years. The value of this approach is that it focuses on the long-term and does not respond to short term fluctuations in population composition. Short-term fluctuations may result from the randomness of the births and deaths, as well as the sex ratio. These fluctuations

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can be particularly pronounced in small populations such as the SRKW. The estimated values of λ average out all these sources of randomness.

The long-term population growth rate (λ) of SRKW is unambiguously lower than λ for NRKW (**Figure 2-3**). These differences in λ result from clear differences in vital rates; SRKW have lower fecundities and survival probabilities relative to NRKW. Life expectancy of females showed large regional effects (37.8 for SRKW vs. 44.9 for NRKW). Expected number of offspring also differs markedly between regions (3.1 for SRKW vs. 3.5 for NRKW). Regional differences in strength of density dependence could not account for the observed differences in population growth rates (Ward et al. 2012a, slide 59).

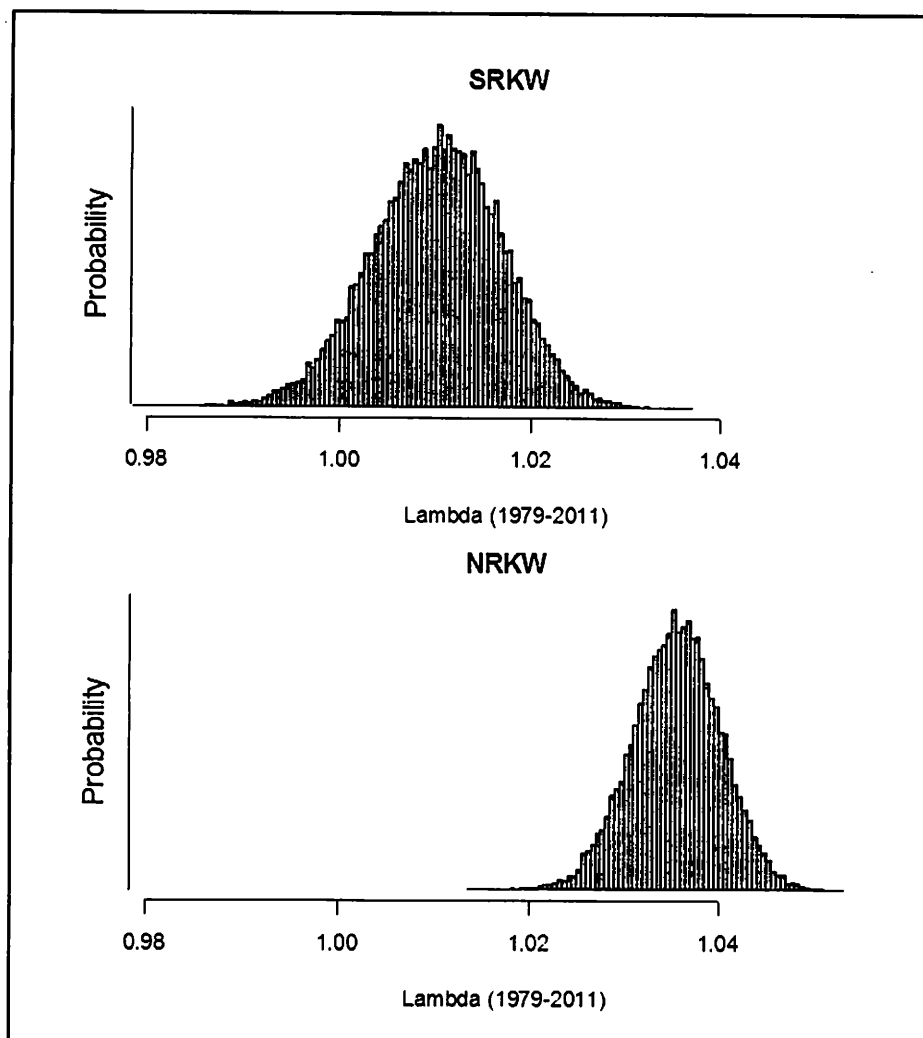


Figure 2-3. Posterior distributions of population growth rate for SRKW and NRKW. The top graph represents the average λ for J, K and L pods. Source: Ward et al. 2012a.

Vélez-Espino et al. (2012) presented an alternative demographic analysis that reached substantially different conclusions than those presented in the first two workshops, which are discussed above. In particular the estimate of λ was slightly less than 1.0 ($\lambda = 0.99$) indicating that, on average, the

population was expected to decline, although the uncertainty in this estimate means that we almost surely cannot rule out positive growth rates. Moreover, the absence of any estimate of uncertainty in the Vélez-Espino et al. estimate means that we cannot know if it is meaningfully different from the Ward estimate.

The Panel concluded that aspects of the Vélez-Espino et al. analysis were problematic. His estimate of λ was not accompanied by any confidence envelope or distribution, making it difficult to evaluate uncertainty. The primary cause for the seeming difference between the two analyses appears to arise from the way that age-specific survival was estimated. The Vélez-Espino et al. method ignored information on the fates of individuals, which is a major strength of the data set. Instead, they

estimated survival for age class i as $\frac{N_{i,t+1}}{N_{i,t}}$. If the abundances were large, this would not be a

problem, especially considering that abundances are measured very accurately, except for sub-yearling calves. However, for small populations, such ratio estimators are not robust representations of population survival rates. For example, if during one year, there was a single death in an age class containing 4 individuals, then the ratio estimate of survival probability would be 0.75. By taking the means of these ratios, this highly uncertain estimate of survival (Figure 2-4, dashed line) would have the same weight in the overall population estimate of survival as 10 deaths out of 40 individuals. Although the two estimates have the same mean, the latter survival rate estimate is more precise (Figure 2-4), and should therefore get higher weight in the overall population estimate. The Bayesian approach presented by Ward et al. (2012a, 2012b) takes advantage of individual animal fates to achieve a proper weighting of information.

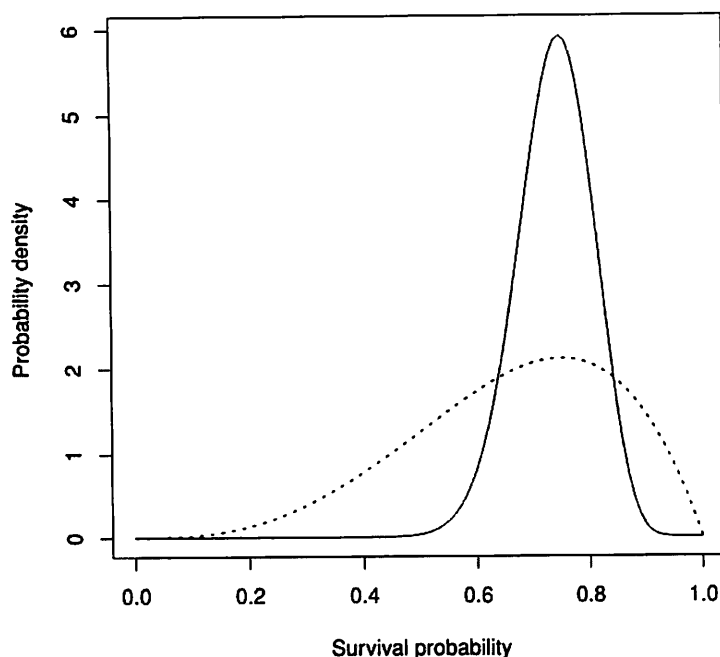


Figure 2-4. Bayesian posterior distributions for survival probability based on 1 death in 4 individuals (dashed line) and 10 deaths in 40 individuals (solid line).

Other issues that need investigation include the consequences of a stage-based model (Vélez-Espino et al. 2012) vs. an age-based model (Ward and Barre 2012, Ward et al. 2012a) and sensitivity to the choice of initial year for the time series of abundance.

It is the conclusion of the Panel that the Vélez-Espino et al. analysis offers alternative perspective. However, it is preliminary. It is the Panel's understanding that the co-authors of this presentation had not yet reviewed it when the material was presented to us. The analyses presented in the earlier workshops had been more thoroughly evaluated, for instance, with major components of these analysis have undergone independent peer review and publication (Ward et al. 2009, 2010b). Thus, the Panel conclusions and recommendations remain focused on the analyses of SRKW demographics, growth rates, and projections models from the Ward presentations (Ward and Barre 2012, Ward et al. 2012a).

Controls on Population Growth Rate

Historic data provide insight into the factors that controlled the population dynamics of NRKW and SRKW. An exhaustive model selection exercise showed evidence for differences in fecundity between southern and northern populations (Ward 2012). The best-supported model included region and indices of salmon abundance as predictors of fecundity, but did not include a density effect. The effect of indices of salmon abundance did not depend on region--- the best model performed better than any model with an interaction term, suggesting fecundity of southern and northern populations responds in a similar way to the prey index. The second best model included male population density and region as predictors.

Models predicting survival from historic data were not easily interpreted (Ward 2012). There were three-way interactions among region, density dependence, and indices of salmon abundance, interactions that could not be understood biologically. Eliminating models with three-way interactions failed to clearly isolate factors controlling survival. The best model showed a negative relationship between female density and survival for NRKW and an inexplicable positive (although weak) relationship between female density and survival of SRKW. The next best model contained a similar response to salmon for NRKW and SRKW and female-based density dependence for both. However, the effect of density dependence varied by region. Effects of female density on survival were far weaker in the southern population relative to the northern population.

The results of analysis of historic data complicate the interpretation of the mechanism presumed to be responsible for the correlation between salmon abundance and killer whale vital rates. The textbook mechanism for bottom-up limitation of predators by prey is that reductions in prey abundance retard the per-capita rate of consumption of prey by predators via their functional response. Reductions in per-capita rate of prey capture, in turn, cause reductions in survival and/or fecundity, thereby reducing population growth via the numerical response. This chain of logic implies that there are *two* ways that the growth rate of predator populations can be increased: (1) by increasing the supply of prey or (2) by reducing the number of predators exploiting the prey. In both cases, per-capita rate of prey consumption should go up leading to enhanced fecundity and/or survival. If the classic mechanism prevails, then we should see support in predictive models of vital rates for effects of prey availability (i.e., the salmon indices, *and* the effect of killer whale density).

However, the effects of density for SRKW were difficult to interpret using the classical line of logic. It is not immediately clear why increases in male density should be more strongly associated with fecundity than increases in female or total density. The weak, positive relationship between SRKW females and survival is contrary to a mechanistic interpretation of functional response influencing the numerical response. The fact that density dependence was stronger in the northern population than in the southern population (Ward et al. 2012a, slide 59) suggests that the northern population should experience stronger bottom-up limitations as the population grows, a prediction that is contrary to observations. All of these difficulties of interpretation cast doubt on a simple, causal interpretation of the positive correlation between salmon abundance and SRKW vital rates. However, the Panel must also point out that the relatively narrow range of density during the period of analysis may mean that there was insufficient statistical sensitivity to detect effects of density.

Population Size and Demography

Evidence for a positive growth rate in populations of SRKW suggests that the population should be increasing, but trends in abundance show little change in population size, particularly during the last decade. This raises the question, why has the population remained small despite a positive growth rate?

The answer to this question appears to come from demography. The K and L pods are each about 60% male which could be the result of demographic stochasticity in the sex ratio at birth and/or juvenile survival. A male dominated population would cause the population to grow more slowly than would be expected if the sex ratio of pods were 50/50 male/females. In contrast, the proportion of females in the Northern Resident population has been increasing recently and in some pods exceeds 60%. Differences in sex ratios between the southern and northern populations may therefore partially explain the differences in their rates of increase and in their abundance.

The primary cause for concern about the viability of SRKW is its small population size. This concern motivated the Panel to ask what is known about the historic size of the population. Demographic reconstruction showed that the largest known size was likely 96 animals in 1967 (Ford and Parsons 2012), leading to the conclusion that the population size has not varied dramatically over the last 45 years.

Synthesis

Understanding the current state of the population of SRKW and the forces that have shaped the current state provides insight into the need to take action to alter the future trajectory of the population. There were two results from the analysis of current status that are particularly compelling. First, analysis of the long-term population growth rate emphasized the importance of properly estimating uncertainty. Although the estimate of the mean λ was strongly positive, the possibility of growth rates less than 1 cannot be ruled out, nor can we reject the idea that long-term growth rates will exceed recovery goals. Second, the absence of a clear negative feedback from population size to vital rates complicates the mechanistic interpretation of a positive correlation between vital rates and food supply. Classical theory in community ecology predicts that reductions

in the number of predators or increases in the number of prey should produce similar responses at the population level. This finding raises doubts about the cause and effect relationship between salmon abundance and killer whale vital rates.

2.4 Recommended Information and Analyses

The Panel recommends that the analysis of Vélez-Espino et al. include estimates of uncertainty in λ and that the analysis undergo peer review.

3.0 FEEDING HABITS AND ENERGETIC NEEDS OF KILLER WHALES

3.1 Context

The apparent specialized diet of SRKW on Chinook salmon while in the southern entrance to the Salish Sea from May to September means that it is biologically plausible for reduced Chinook salmon abundance to cause nutritional stress and impede recovery of the SRKW population. Considerable research has been undertaken by NOAA, DFO, NGOs, and others to assess the mechanistic link between Chinook salmon abundance and the demographic dynamics of SRKW. This research has sought to determine whale distribution, diet composition, metabolic requirements, and indicators of nutritional stress—and explore whether salmon abundance is low enough to cause such stress in SRKW.

Distribution. J, K, and L pods typically feed in the inland waters of Washington State and British Columbia (Strait of Georgia, Strait of Juan de Fuca, and Puget Sound) from late spring to fall (Bigg 1982, Ford et al. 2000, Krahn et al. 2002). They are known to visit coastal sites off Washington and Vancouver Island (Ford et al. 2000, Krahn et al. 2004), and to travel as far north as Southeast Alaska (Chatham Strait), and as far south as central California. Winter and early spring movements and distributions are largely unknown—however, limited data from acoustic monitoring, photo-identification and contaminant signatures in blubber suggest some individuals spend substantial time in coastal waters off the coasts of Washington, Oregon and northern California (Krahn et al. 2002, 2009, Riera 2012)

Diet (Species & Size Selectivity). Limited dietary information based on identification of scales, tissues, and fecal DNA suggests that SRKW primarily consume large Chinook salmon from late spring to fall, and lesser amounts of chum salmon in fall (Ford and Ellis 2006, 2011, Ford et al. 2009, 2010b, Hanson et al. 2010a, 2010b, 2010c, Hanson 2011, Ford 2012a). Other salmonids (coho, steelhead, sockeye, and pink) and other non-salmonids (herring, rockfish) appear in diets occasionally. Stomach contents from a limited number of dead stranded resident whales have contained squid beaks (Ford et al. 1998), which suggests that other non-salmonid prey are occasionally ingested. Winter diets remain poorly described, but are believed to be more diverse than in summer and consist of smaller Chinook salmon and greater numbers of non-salmonids (ling cod, dover sole, and halibut) than observed during the summer and fall.

SRKW have strong preferences for larger-bodied organisms, which in the case of Chinook salmon, tend to be energetically denser than smaller prey. The age distribution of Chinook salmon consumed by SRKW does not match the age distribution of Chinook salmon thought to be available to killer whales (as predicted by the fisheries management model, FRAM; Ward et al. 2010a). Instead, SRKW consume greater proportions of the larger (older) fish (particularly the 4- and 5-year-olds) relative to the overall numbers of Chinook salmon present. They also seem to feed mainly on salmon bound for the Fraser River during the summer, and appear to take less of the Puget Sound Chinook salmon (Ford and Ellis 2006, Hanson et al. 2010a, Parken et al. 2011, Warheit

2012). Unfortunately little is known about diet and salmon selectivity during winter—an important uncertainty given the variation in energy density among Chinook salmon stocks and the need to understand energy intake and identify the critical Chinook salmon stocks SRKW rely upon.

Daily Prey Requirements. The amount of Chinook salmon required by SRKW was estimated by NOAA using a bioenergetics model (Noren 2011a, 2011b) for three time periods (October–April, May–June and July–September) based on the proportion of Chinook salmon in the diet, daily energy requirements and time spent by SRKW in inland waters. The stock-specific consumption for SRKW in the summer was also estimated (Hanson et al. 2011). DFO concurrently estimated the number of Chinook salmon needed by Resident killer whales using the Noren bioenergetics model (Ford et al. 2010b), while Williams et al. (2011) estimated SRKW Chinook salmon requirements under a range of scenarios using morphometric data from Icelandic whales and captive killer whales. All of the estimates of daily prey energy requirements are sensitive to the body size of the whales and the calorific content of the Chinook salmon—as well as the proportion of diet that is assumed to be Chinook salmon. Lactation is a significant energetic cost for females with calves, but does not contribute significantly to the estimated prey requirements of the overall population because few individuals are lactating at any one time.

Nutritional Stress. Photographs of thin whales and observations of the “peanut-head syndrome” (loss of the nuchal fat pad behind the skull) in SRKW suggest that a few individuals in some seasons are significantly emaciated. Such weight loss can arise from a variety of causes that range from malnutrition due to food shortage, to malnutrition secondary to infectious disease, parasitism or chronic degenerative processes. In wild mammals, the most commonly recognized cause of generalized weight loss is food shortage (e.g., King and Murphy 1985, Trites and Donnelly 2003, Schultner et al. 2012).

Body condition of marine mammals can range widely among individuals within a population, and social factors such as prey sharing may complicate identifying relationships between prey availability and nutritional status of an individual. Little is known about the factors that influence body condition of wild whales, although correlations between body shape and environmental conditions have been made for baleen whales, with one study indicating that weight loss behind the skull (“peanut head”) of gray whales (*Eschrichtius robustus*) is associated with lactation in adult females (Bradford et al. 2012), while another study concluded that body condition varies with the duration of the previous feeding season (Perryman et al. 2002).

The presence of emaciated whales in the SRKW population that have subsequently disappeared indicates that some individuals in poor condition may have experienced nutritional stress, although it remains unclear whether it is a seasonal and frequently occurring phenomenon in SRKW. It also remains unclear what caused the poor condition of these animals, and what the background rates of this syndrome are. A major challenge in interpreting data on the incidence of “peanut-head syndrome” or other indicators of nutritional stress is identifying the baseline against which to compare new observations because all wild populations encounter periods of nutritional stress. Poor condition and nutritional stress could contribute to increased mortality or reduced fecundity of SRKW through a variety of mechanisms (i.e., direct starvation, increased susceptibility to trauma due to increased foraging movements, decreased resistance to infectious disease, mobilization of

lipophilic toxic chemicals, etc.). Poor condition and nutritional stress could also decrease recruitment through changes in calving intervals and calf survival. Indicators of nutritional stress in individual whales include behavioral, morphological, hormonal, and reproductive changes that can be assessed with a variety of methods. However, prey sharing (documented to occur about three-quarters of the time; Ford and Ellis 2006) complicates understanding the effects of prey limitation on some individuals of the SRKW population, especially adult females that do more sharing.

The effect of prey sharing on the association between food limitation and body condition could accentuate individual differences in body condition if animals continue to share prey at the expense of their own loss of condition and allow the receiving individual to gain weight. Conversely, prey sharing could mask individual differences in body condition if more successful animals that are in better condition share prey with thinner individuals. Thus, the influence of food availability on the social structure of resident killer whales (Foster et al. 2012) confounds the relationship between food availability and nutritional condition among individuals and complicates making simple conclusions about the causes of any changes observed in the body condition of SRKW.

3.2 Key Questions

Diet composition, foraging distributions and metabolic requirements of SRKW outside of the summer months are not well described because these data are difficult to obtain and have been gathered opportunistically rather than collected following a statistical design. Considerable effort has been directed towards determining diet composition and selectivity, particularly on Chinook salmon. The Panel was asked whether the approaches and methods used to estimate diet composition and selectivity were scientifically reasonable and whether these techniques could be improved. The Panel was also asked to assess the conclusion that SRKW eat mostly Chinook salmon during the summer and fall in the Salish Sea.

In terms of the prey requirements of SRKW, the Panel was asked to assess whether the bioenergetics modeling approach used to estimate energy needs was a scientifically defensible approach and whether there were additional refinements that could be made to improve these estimates of predatory demand on Chinook salmon in the Salish Sea. The Panel was also asked to evaluate whether ratios of energy needed by SRKW to the energy available from Chinook salmon in the Salish Sea were a reasonable and defensible way to assess the adequacy of Chinook salmon stocks for sustaining and rebuilding SRKW.

Finally, the Panel addressed whether behavioral, hormonal, or estimates of body condition were useful metrics for assessing nutritional stress in SRKW relative to seasonal and inter-annual variation in prey availability.

3.3 Responses to Key Questions

Diets of Southern Resident Killer Whales

Diets of SRKW have been determined from scales and tissue recovered from salmonid prey that are broken up near the surface for sharing among individuals. Diets have also been determined from the stomach contents of dead whales, and from the prey DNA in fecal samples. These quantitative molecular methods used on individual samples are solid and state of the art. However, collecting samples is difficult and the descriptions of diet are not necessarily representative of the entire population given the concentration of effort in the summer through autumn months, with little or no coverage in the winter months. Furthermore, biases associated with likelihood of prey being shared, digestibility of prey and amount of DNA per sample will influence results. The Panel believes that, despite the logistical challenges of collecting diet samples, the existing data offer a reasonable indication of summer diets of SRKW in the Salish Sea.

The winter ecology of SRKW after leaving the Salish Sea differs from their summer ecology, but there is little information about diet composition and selectivity in winter months. Given the general absence of the whales from the Salish Sea in winter, they are less likely to consume significant amounts of Fraser River salmon. However, winter diet composition is a major source of uncertainty in understanding the foraging ecology of SRKW.

The majority of dietary data show that SRKW and NRKW have a preference for salmon, particularly large Chinook salmon which appear to account for >80% of the diet from May–September. The general conclusion that SRKW consume primarily large Chinook salmon (4- and 5-year-olds) is reasonable and supported by the available information. It is conceivable that smaller Chinook salmon may not be shared as readily and could be swallowed whole without much handling—a factor that could bias detecting the presence of Chinook salmon in the diet from tissue and scale data (Hanson 2011). Fecal DNA samples can detect the presence and proportions of Chinook consumed, but cannot provide information about their sizes. Some groundfish could also be swallowed at depth without being brought to the surface, and would not be detected by scale and tissue sampling. Fecal DNA testing can overcome this potential sampling bias (although digestion may obscure the passage of DNA from some prey species).

The samples obtained in Puget Sound during early winter (October–December) suggest a greater reliance by SRKW on chum salmon and on demersal species during winter, although 24 samples collected in coastal waters indicate a predominance of Chinook salmon in the diet (Hanson 2011). The paucity of winter diet data outside of Puget Sound limits the ability to assess the degree to which SRKW rely on chum salmon, smaller Chinook salmon, or other fish species during this potentially challenging time of year.

Biopsy samples from some individual SRKW give indirect information about diet for a small number of years. Limited data on nitrogen stable isotope ratios in skin samples suggest that L pod may have changed its dietary trophic level over the last decade (O'Neill et al. 2012a). The isotope ratios also suggest that the diet trophic level of K pod varies seasonally. Fingerprints of lipophilic contaminants in blubber biopsies also provide insight into diets. Ratios of these contaminants

found in the blubber of K and L pod match with similar ratios of prey species in California as indicated by the relatively high concentrations of DDT, suggesting that fish from California form a significant component of their diets (Krahn et al. 2007, 2009, O'Neill et al. 2012b).

Though logistically challenging, future research on diets of SRKW should expand seasonally and include winter surveys, ideally reflecting temporal and spatial distribution of the whales. Further refinement of the currently employed methodologies and sampling designs are likely to show a more complex and diverse diet related to age, sex, pod and time of year than presently recognized. However, further diet studies are unlikely to change the fundamental finding to date that Chinook salmon are the most important component of the SRKW diet. Instead, they should provide data needed to determine whether SRKW can adapt alternative foraging strategies during times when Chinook salmon are rare by consuming alternate prey at rates that do not compromise their fitness, or by moving outside of the Salish Sea to consume other stocks of Chinook salmon (Hanson et al. 2012).

Diet analysis that determines the frequency with which species of prey occur in stomachs or fecal samples requires ~70 samples by season to accurately describe diet (Trites and Joy 2005). A sampling design should be implemented with a coordinated effort to collect the necessary numbers of samples. Additional insights into diets of SRKW can be obtained from killer whale blubber and skin samples through analysis of contaminant ratios, stable isotopes and fatty acid composition. Direct observation of predation by SRKW relative to potential prey sources also contributes useful information about diets and preferences.

Energy Needs of Southern Resident Killer Whales

The modeling approach used to estimate the food requirements of SRKW is sound and consistent with the models that have been developed for other species of marine mammals. It yields reasonable estimates of energy needs, although there is considerable uncertainty due to uncertainty in some of the parameter estimates and assumptions made. The estimated energy requirements of SRKW have been derived using the best available data, and can only be refined by incorporating better parameter estimates for such variables as body mass at age, activity, seasonal changes in body condition, and basal metabolic rates. Such model refinements will come with time and will improve confidence in the estimates of energy needs. Nevertheless, the numbers of fish that NOAA and DFO estimate that SRKW require are within reasonable limits.

In addition to refining model parameter estimates, seasonal variability in energy requirements is a key uncertainty that still needs to be addressed. Photogrammetry data could be used to determine whether seasonal changes in body condition occur (as suggested by seasonal changes in fecal hormones; Ayres et al. 2012). Additional photogrammetry data would contribute to determining whether there is a relationship between body condition and seasonal changes in energy requirements due to differences in reproductive stage, movements and daily activity budgets. It would also contribute to identifying possible mismatches in seasonal prey availability with seasonal energy requirements that could have significant physiological effects on fecundity or susceptibility to disease. Photogrammetry data could also be used to investigate body condition changes in years of high versus low Chinook salmon abundance.

Photogrammetry appears to be a promising technique to detect changes in body shape (Durban et al. 2009, 2012), and could be further refined using captive killer whales. A systematic use of photogrammetry to evaluate seasonal and annual changes in individual whale body condition can provide key data to assess the nutritional status of SRKW relative to population recovery. However, this use of photogrammetry assumes that changes in condition can be causally linked to changes in individual reproductive success and survival.

Ratios of Energy Needs to Energy Available

The ratios of energy needed by SRKW to the energy available to them from Chinook salmon are not particularly useful for understanding whether fisheries for Chinook salmon affect the population dynamics of SRKW. Simply put—there is no objective means to evaluate the biological significance of the ratios on the status of SRKW. The forage ratios therefore provide little insight into possible prey limitations faced by SRKW, and require knowing whale fitness or vital rates as a function of the supply-to-demand ratios to be useful. The ratio cannot be interpreted without having such a functional response (unless it is < 1 and clearly indicative of a prey deficiency).

Comparisons between the SRKW and other apex predators in other ecosystems are also not well justified, and are again difficult or impossible to interpret without knowing what demands are placed on Chinook salmon (or any prey) by the entire community of predators that feed on them (the predator demand component of the ratio). It is possible, for example, that killer whales consume a larger component of the Salish Sea Chinook salmon stocks because the Salish Sea is home to fewer other important apex predators compared to other ecosystems.

Calculating ratios does not appear to provide any meaningful information about either the ecosystem or the biology of SRKW. Continuing to undertake this analysis is not warranted. Such analyses might provide some insights into the ecology of the Salish Sea ecosystem if directly comparable models are generated for other species in the Salish Sea or other ecosystems (i.e., same assumptions, taxonomic resolution, etc.). The calculated ratios (Noren 2011b, Williams et al. 2011) have been derived from many disparate models with very different assumptions.

Nutritional Stress

The available information on body condition of individual SRKW (Durban et al. 2009, 2012) documented 13 members of the SRKW population in poor condition using boat-based photographs obtained from May–September over the period 1994 through 2008. All but two of those individuals subsequently died. None of the individuals that died were recovered and examined, so definitive date and cause of death are unknown. However the implication from these data is that some SRKW have been nutritionally limited at certain times of year.

The data available on fecal hormone levels are not clearly indicative of nutritional stress in the SRKW population. Measurements of fecal hormones can give valuable insight into the physiological status of individual animals and populations. Triiodothyronine (T3) and corticosterone concentrations in fecal samples collected over three years from killer whales from all three SRKW pods suggest seasonal changes occur in fecal T3, with a decline in values from spring through

summer to fall (Ayres et al. 2012). This change could be explained by changes in photoperiod, as well as by individual differences in nutritional status, age, sex, reproductive status, stress and PCB exposure of individuals sampled (St. Aubin and Geraci 1988, 1989, Fair et al. 2011, Schwacke et al. 2012). Changes in photoperiod are major drivers of thyroid gland function (Walton et al. 2011), which is consistent with the reported linear response of T3 in the SRKW to Julian date (Ayres et al. 2012). Unfortunately, the lack of fecal hormone data in winter months due to logistical difficulties associated with sample collections limit the interpretation of the available fecal hormone data to assess the nutritional status of the SRKW.

Although nutritional status can influence fecal thyroid hormone levels, other factors such as age, activity, day length, water temperature, reproductive status and contaminant exposure also affect fecal hormone levels (Oki and Atkinson 2004, Ciloglu et al. 2005, Ross et al. 2007, Fair et al. 2011). It is thus uncertain whether the seasonal change reported in fecal thyroid hormone levels indicates nutritional stress or a seasonal endocrine shift associated with other factors.

Cortisol levels are indicative of activation of a stress response, which is a common physiological pathway that results from any stressor (in addition to nutrition) such as sound, boat traffic, or conspecific aggression. Use of fecal cortisol alone as an indicator of nutritional stress is therefore limited in an environment with considerable human activity.

Social behavior and group sizes may also be altered by changes in nutritional status and the availability of prey (Lusseau et al. 2004). Low availability of Chinook salmon and a long-term reduction in returning stocks of Chinook salmon appear to have reduced social cohesion in SRKW (Parsons et al. 2009) and increased movements of SRKW in the San Juan Islands (McCluskey 2006). Changes in social behavior may thus be more sensitive indicators of nutritional limitation than changes in fecundity or survival for SRKW.

3.4 Recommended Information and Analyses

Diet Analysis

A shortage of samples during winter is the biggest gap in diet studies of SRKW. Increased effort is needed to obtain winter samples (November–May). One approach is to satellite track tagged individuals to determine where fecal, tissue and scale samples can be collected. However, this is logistically difficult and can impact the behavior of individual animals that are tagged.

A second limitation of current understanding of killer whale diets is that tissues and scales recovered in the water column after food sharing are likely biased towards salmonids. More fecal sampling is therefore needed to detect the prevalence of non-salmonids, and determine the extent to which tissue and scale sampling might be biased by prey sharing. The utility of fecal sampling could also be evaluated by feeding known prey to killer whales in aquaria and collecting and analyzing their fecal DNA.

A third recommendation is to continue archiving fecal and blubber samples from future stranded animals in addition to stomach contents. Dietary analysis of these samples can be compared with

those obtained from stomach content analysis. The full thickness of the blubber should also be archived for future dietary analyses using fatty acids.

Finally, more effort could be expended on contaminant fingerprinting techniques that hold substantial promise for improving estimates of SRKW diets and identifying likely feeding locations based on the similarity between their contaminant fingerprints and the fingerprints of their available prey.

Energetic Needs

Satellite tagging of whales in winter and continued acoustic monitoring outside the Salish Sea is needed to identify winter foraging areas and estimate the range of movements to determine activity budgets and better estimate the prey requirements of SRKW. In addition, future analysis of foraging behaviors is needed to detect potential changes in activity budgets (proportion of time spent foraging, socializing, resting, and travelling), movement patterns (frequency and duration of excursions outside of regular feeding areas), dispersion (spreading out if prey density is low), foraging success (lower catch per unit effort when prey availability is low), and prey switching (increased predation on alternative prey if Chinook salmon density is low). However, interpreting changes in behavioral patterns as simple indications of nutritional (or other) stresses will be a continual challenge.

Nutritional Status

Overall, the Panel believes that increased use of photogrammetry to monitor seasonal and inter-annual changes in growth and body condition of SRKW is likely to yield the greatest number of new insights into the foraging ecology of SRKW. Research designed to monitor nutritional status of SRKW should focus on refining and evaluating current photogrammetry methods (e.g., Durban et al. 2009, Fearnbach et al. 2011) to evaluate the utility of different morphometric indices as measures of nutritional status. Research should also undertake longitudinal sampling to investigate seasonal changes in body condition of individuals, and at-risk age- and sex-classes. In addition, analysis of individual calving intervals, group sizes, and association strengths should be assessed as measures of relative feeding conditions. Changes in social cohesion may be a sensitive indicator of nutritional stress in SRKW (Foster et al. 2012). Photogrammetric surveys should be coordinated with biopsy sampling to enable comparisons with the more direct measures of nutritional status.

4.0 FISHERIES AND PREY AVAILABILITY

4.1 Context

The Panel was asked to evaluate the available information and analyses concerning abundance and distribution of Chinook salmon, distribution of SRKW, and how fisheries may affect the availability of Chinook salmon to SRKW in their summer critical habitat and in coastal waters where SRKW are found during other months. The Panel was also asked to assess the possible increases in ocean abundance of Chinook salmon that might result if ocean and/or freshwater fisheries were closed and/or modified. The Panel does not pass judgment, in this section, on the issue of whether or not possible increases in ocean abundance would materially increase the probability or speed of recovery of SRKW.

Historic vs. Current Abundances and Marine Distribution of Chinook Salmon: The “Big Picture”

Myers (2011) presented “back of the envelope” calculations (based on cannery records and various assumptions regarding relationships between numbers of fish processed and cannery records) of historic (1890-1920) abundances of Chinook salmon in the mainland US, coastal British Columbia and the Fraser River. These estimates suggest that historic abundances were dominated by fish from the Columbia River (4.6 million), California’s Central Valley (1.1 million), and Coastal British Columbia stocks (Skeena + “Outlying Area” = 1.2 million), with the Fraser River (0.55 million) and Puget Sound (0.69 million) making substantial contributions as well.

Contemporary abundances of Chinook salmon in the Pacific Northwest and California have been greatly reduced from these historic abundances and many Evolutionarily Significant Units (ESUs) of Chinook salmon are listed as threatened or endangered under the US Endangered Species Act and many British Columbia stocks have been identified as of stocks of conservation concern. (Indeed, one wonders if recovery of some of these Chinook salmon populations is limited by killer whales and increasing populations of harbor seals and sea lions (Lessard et al. 2005).) As noted by Myers, declines in spring-run fish have been dramatic in many river systems, in part because the historic spawning grounds of these fish are today often above impassable dams. Declines in abundance of spring-run fish have been particularly evident in California’s Central Valley, in the Columbia River (interior spring Chinook salmon) and in Puget Sound. Coastal British Columbia populations from the Skeena and “Outlying Areas” have experienced declines in abundance and declines in abundance have been alarming in southern British Columbia.

Associated with the declines in abundance have also been shifts in age structure of many populations toward younger age and smaller adults. Such shifts have ranged from fairly modest (e.g., Willamette River spring-run) to quite striking (e.g., California’s Central Valley). In many of today’s Chinook salmon populations (including those from California’s Central Valley, see Myers 2011, slide 13), age-5 adults are rare and age-6 fish are virtually nonexistent, though historical

records from the same populations indicate that age-5 fish were common and age-6 were regularly present².

Recoveries of coded-wire tagged (CWT) hatchery Chinook salmon in ocean fisheries have provided strong evidence that marine distributions vary substantially according to stock of origin. Early analyses of CWT recoveries from California and Oregon coastal stocks suggested that Chinook salmon stocks south of Oregon's Cape Blanco are "south-migrating" fish that are captured almost entirely from central Oregon through central California (Nicholas and Hankin 1988). Northern Oregon Coastal stocks, and most late-maturing Columbia River fall Chinook salmon stocks are "far north-migrating" and are captured in ocean fisheries in "outside coastal waters" off Washington, British Columbia and Alaska. More recent and more extensive analyses of CWT recovery patterns for Chinook salmon stocks (Weitkamp 2010) have revealed a dozen distinctive patterns of ocean recoveries which appear related primarily to the geographic area from which stocks originate. One interesting generalization for north-migrating stocks is that older fish tend to be caught further north from their river of origin than younger fish. Although most Chinook salmon stocks seem to have relatively nearshore coastal distributions that make them highly vulnerable to ocean troll fisheries, stream-type spring-run Chinook salmon from the Interior Columbia system and from the Fraser system appear to have a non-coastal ocean distribution (Myers 2011). Marine fishery impacts on such spring Chinook salmon stocks are very minor and availability to killer whales would be largely limited to terminal areas as mature fish.

Recent Trends in Chinook Salmon Abundance and Fisheries

Kope and Parken (2011) summarized trends in abundance and fishery catches of Chinook salmon for various aggregates for the period 1979 to the present. The period begins with the first years of fisheries regulated under the 1976 US Fisheries Conservation & Management Act which established the Pacific Fisheries Management Council, and also is a period of time during which fisheries managers have relied very heavily on recoveries of coded-wire tagged hatchery fish to serve as indicators of exploitation history for many natural-origin Chinook salmon stocks. Comparing averages for 2001-2010 with those for 1979-1988 and considering stocks of likely importance to the SRKW, Kope noted that: (1) Fraser Early Chinook salmon total abundance (terminal run + fishery impacts) has increased by about 36%, and terminal run size has increased by more than 100%; (2) West Coast Vancouver Island aggregate total abundance has decreased by 35%, but terminal run sizes have increased by about 19%; (3) Fraser Late Chinook salmon total abundance has decreased by about 51%, but terminal run size has increased by about 38%; and (4) Puget

² Throughout this section, we denote ages of Chinook salmon in total years, equivalent to a tacit assumption that the vast majority of Chinook salmon stocks that may be available to SRKW are ocean type Chinook salmon for which juveniles outmigrate as sub-yearlings. We recognize, of course, that some important Chinook salmon stocks have primarily yearling smolts and that size and maturity at total age is different for these stocks than for ocean type stocks with sub-yearling smolts. Most such stream type stocks are spring race Chinook salmon which, as noted below for upper Columbia stocks, typically have little availability to ocean fisheries and would therefore presumably have little availability to SRKW in coastal waters. These stocks would be available to SRKW only when they passed by foraging whales on their return to spawning streams as mature fish.

Sound total abundance has decreased by about 38%, but terminal run size has not changed. Coast-wide, Kope noted an approximate 16% decrease in total Chinook salmon abundance, but a concurrent 37% increase in ocean escapement to terminal areas. These shifts toward larger terminal run sizes reflect changes in management policies that have responded to: (a) unacceptably high ocean fishery exploitation rates on certain Chinook salmon stocks³; (b) legal requirements for catch sharing of certain stocks between ocean fisheries and terminal net fisheries (Native American and First Nations fishing rights); and (c) weak stock management policies designed to improve conservation status of ESA-listed populations of Chinook salmon (US) or DFO-identified stocks of concern (Canada). Long (WDFW; 2011) provided a very detailed review of substantial reductions in marine fisheries catches that have taken place in the immediate vicinity of the summer feeding area of the SRKW (i.e., in the Strait of Juan de Fuca and around the San Juan Islands).

Van Will and Adicks (2011) summarized recent changes in abundance and fisheries for other salmon species that are present in diets of SRKW, though at lower prevalence (chum salmon) or very low prevalence (coho salmon, sockeye salmon, steelhead trout). Aggregate escapement of “inside southern chum” (a British Columbia group which moves between Vancouver Island and the mainland) has averaged about 3.5 million (catch + escapement), with an apparent increasing trend from 1965 through 1999. Puget Sound fall chum enter the eastern Strait of Juan de Fuca and Puget Sound during September through December and are the most abundant run type (average run size of 1-2 million). Abundance of these fish has generally increased over the period 1968 through 2009.

LaVoy (2011) presented a FRAM-based analysis of possible increases in kilocalories of Chinook salmon that might be generated from various levels of fishery closures, and Hagen-Breaux (WDFW; 2012) presented a simplified assessment of the probable effects of fishery closures on total abundance (numbers) of mature age-4 and age-5 Chinook salmon from “inland stocks” (Puget Sound + Fraser early run, Fraser late run, Lower Georgia Strait stocks). When all ocean fisheries for Chinook salmon (Puget Sound, all US + Canadian) were closed, average increases in Chinook salmon abundance were about 20% for all inland stocks combined, with increases to Fraser stocks of about 15%, but with only about 3.5% increase in Puget Sound Chinook salmon.

Geographic Distribution of SRKW and Probable Overlap in Distribution with Chinook Salmon Stocks.

Barre (2011) gave an overview of the NOAA Recovery Program for the SRKW, indicating that the range of this population extended from the Queen Charlotte Islands in British Columbia to central California, with the San Juan Islands in Puget Sound being a May–September “hot spot”. Designated Critical Habitat (under the ESA) for the SRKW was defined as the US side of the Strait of Juan de Fuca, Puget Sound, and regions around the San Juan Islands to the Canadian border, and similar Critical Habitat has been defined in Canada under SARA. Hansen and Emmons (2011) summarized

³ Throughout this report, we use the term “ocean fishery exploitation rate” to mean the probability that an age *i* salmon, present in the ocean when the ocean fishing season begins, is harvested in the ocean at age *i*. For Chinook salmon, ocean fishery exploitation rates on age-2 fish are generally close to zero and exploitation rates for age-3 fish are usually about 50%-75% of those for age-4 and older fish.)

characterizations of the geographic distribution of SRKW based on available sightings data, with a focus on time spent in critical habitat during summer and fall months, and provided an initial summary of findings from passive acoustic recorders that allow identification of SRKW vs. NRKW by vocalizations. Ford (2012b) presented evidence that the winter distribution of SRKW (L pod) may range as far north as Pt. Ellis, Alaska, about 275 km north of the Queen Charlottes. Ford et al. (2012) presented a more complete review of information on SRKW geographic distribution, including summaries of whale detections from the coastal sighting network (CWR) and DFO as well as from NMFS passive acoustic recorders that have been deployed at various locations off the coasts of Washington, Oregon and California. Ford et al.'s presentation suggested that SRKW are found almost exclusively in the Salish Sea and/or in coastal waters near the entrance to the Strait of Juan de Fuca during the July–September period (Ford et al. 2012). During the April–June period, only about 32% of SRKW sightings have been in the critical habitat area with remaining sightings primarily in coastal waters off northern Oregon and Washington and outside waters of Vancouver Island. During late fall (October–December) relatively few sightings (19%) have been from the critical habitat area and during winter months (January–March) almost no sightings (4%) have been made in the critical habitat area. During winter months SRKW are sometimes distributed off of central California, though more frequently they seem found off the Washington coast.

Ford et al. (2012) also presented some conjectures concerning the overlap in the geographic distribution of SRKW and Chinook salmon stocks, based on a comparison between Weitkamp's (2010) CWT-based assessment of Chinook salmon distribution patterns and available information concerning geographic distribution of SRKW. Ford et al. (2012) concluded that SRKW distribution overlaps with "all major stocks from south of central BC" during the April–December period, although certainly degree of overlap would be stock-dependent, being much less for California Chinook salmon stocks, for example, than for Washington coastal stocks. Available data concerning winter (January–March) distribution of Chinook salmon are inadequate (due to fishery closures during this period) to allow assessment of winter distribution patterns of Chinook salmon and data on winter distribution of SRKW are also limited, so it is not possible to reliably assess the possible degree of overlap of SRKW and Chinook salmon during this period.

4.2 General Comments

There is no question that contemporary abundance of Chinook salmon in the Pacific Northwest is small compared to historic abundance, with greatest reductions in abundance for spring-run Chinook salmon from the Columbia River system. According to Kope and Parken (2011), however, changes in coast-wide abundance of Chinook salmon populations over the past 30 years, the period of time over which status of SRKW has been closely monitored, have been relatively modest: an approximate 16% decline in total abundance, but with a corresponding substantial 37% increase in terminal abundance (returns to freshwater) due to increased restrictions on marine fishery harvests.

There seems no question that during the summer period (July–September), when the SRKW spend almost all of their time in the areas that have been designated as Critical Habitat, the SRKW population must be foraging primarily on maturing Chinook salmon that are entering the Strait of

Juan de Fuca or Georgia Strait on their return to freshwater streams of origin, primarily streams that enter Puget Sound and the Fraser River. Therefore, during the summer period it seems fairly clear that a rather limited set of Chinook salmon stocks would be directly exposed to predation by the SRKW, that mostly mature (rather than immature) individuals from these stocks would be available, and that only fisheries that impacted these specific stocks would affect prey availability during the summer period⁴. Warheit (2012) presented evidence that the genetic composition of the Puget Sound recreational Chinook salmon fishery was dominated by Puget Sound Chinook salmon, in contrast to diet of SRKW which was dominated by Fraser River fish. Careful inspection of the distribution of recreational fishermen as compared to foraging SRKW suggests that extensive foraging on Fraser Chinook salmon is a consequence of the coincident geographic locations of foraging SRKW and the frequent migration path of Fraser Chinook salmon through Haro Strait. If the summer period were the critical foraging period for SRKW, these observations would strongly argue for exploration of a possible link between SRKW performance attributes (net reproductive rates, survival rates) and terminal run size (i.e., mature fish only) of a very limited number of relatively well-identified Chinook salmon populations, mostly of Fraser River origin.

If instead SRKW rely primarily on Chinook salmon during the winter period and if the winter period is the critical period with respect to energetic needs, with the possibility of poor condition leading to increased death rates or decreased fecundity, then one might instead argue that SRKW vital rates should be related to some larger and likely complex aggregate of the abundances of many different Chinook salmon stocks from at least northern Oregon through southern British Columbia. The extent to which SRKW depend on Chinook salmon during the winter period is poorly identified, however, as are the geographic and temporal distributions of both Chinook salmon and SRKW during the winter period. It does seem clear that the SRKW are more often found in coastal areas (e.g., Washington coast) than in the designated critical habitat during the winter months, but existing winter distribution data also suggest substantial inter-annual variability in geographic distribution. It does seem reasonable to believe that Chinook salmon populations with ocean distributions typically north of the most northern detections of SRKW would be ruled out as important contributors to SRKW diet and that southern Oregon and California Chinook salmon populations would not be of importance except during those years when SRKW moved to southern Oregon or California waters during winter. Weitkamp (2010) provides a helpful guide for conjectures regarding stocks likely to have substantial winter overlap with SRKW, but little confidence could be placed in such conjectures due to poor winter distribution information for both SRKW and Chinook salmon stocks.

⁴ Based on genetic analysis of SRKW feces and scale samples collected from kills during summer months (Hanson 2011), it seems clear that Fraser River stocks dominate SRKW Chinook salmon consumption during summer months, with Fraser spring stocks most important during May and June.

4.3 Key Questions and Responses

1) Do any parts of these data need further clarification?

Chinook salmon abundance indices and their use in assessing influence of Chinook salmon abundance on SRKW vital rates.

In the Panel's report following Workshop 1, substantial attention was devoted to: (a) discrepancies between estimates of Chinook salmon abundance generated using the FRAM model and the CTC-generated abundance indices for stock aggregates; (b) inconsistencies in statistical inferences concerning the effects of Chinook salmon abundance on SRKW "fecundity" (net reproductive rates) and survival rates based on the two alternative abundance indicators; and (c) concerns relating to whether Chinook salmon available to killer whales were generally mature/maturing as compared to immature fish. The Panel also expressed concerns about how selectivity functions had been developed and used to account for the apparent preference of killer whales for larger and older Chinook salmon.

These initial Panel concerns were prompted by an implicit (and possibly incorrect) initial supposition that SRKW foraging during the summer period was of primary concern and interest. Given the consistent findings that SRKW foraged extensively in the designated critical habitat during summer and early fall months and primarily consumed Chinook salmon during this period, and assuming that successful foraging during summer months was critical to the survival and fecundity of SRKW, it was natural to devote attention to which of the two abundance indexes (CTC or FRAM) might be better suited for allowing identification of the abundance of mature Chinook salmon from a relatively small number of stocks that would contribute to summer diet of SRKW (those passing by the critical habitat on return to their spawning grounds as mature fish).

Following Workshop 1, there was substantial response to the Panel's concerns regarding the FRAM and CTC indicators of Chinook salmon abundance and Workshop 2 provided Panel members with an improved ability to interpret these abundance indices and to assess their possible use for representation of Chinook salmon available to SRKW. Several presentations were made at Workshop 2 that clarified the key assumptions and limitations of three abundance indices: FRAM, CTC, and a new Kope-Parken index. Specifically, Ward and co-authors presented revised logistic regression analyses relating the Kope-Parken run reconstruction-based measures of terminal run size and total ocean abundance metrics to SRKW "fecundity"⁵ and survival rates, along with a comparison of results with those based on FRAM and CTC indices (Ward et al. 2012b); Hagen-Breaux presented a simplified application of FRAM (as noted above) (Hagen-Breaux 2012); and LaVoy presented a useful overview and contrast of the FRAM, CTC, and Kope-Parken procedures (LaVoy 2012).

⁵ The term "fecundity" is used in this section as equivalent to "net reproductive rate" – the number of young produced annually per female that survive to be alive when whales are first fully "counted" during early spring.

With respect to assessing the potential impact that abundance of Chinook salmon stocks might have on SRKW vital rates, *assuming that the summer period is key*, the Panel believes that the Kope-Parken metrics of terminal abundances (for stocks passing through the critical habitat area) seem more appropriate than the original FRAM-based metrics, and that the aggregated CTC indexes do not seem appropriate for such a purpose.

With respect to assessing the potential impact that availability of Chinook salmon stocks might have on SRKW vital rates, *assuming that the non-summer period is key*, the Panel believes that the relative merits of the three abundance indices are quite different than for evaluation of the summer period. In this context, all three abundance metrics could plausibly be used to develop measures of Chinook salmon abundance that might be tied to SRKW vital rates because during the non-summer months the SRKW exhibit a broad and highly variable coastal distribution.

Ward et al. (2012b) suggested that effects of Chinook salmon abundance on “fecundity” and survival rates were relatively consistent between CTC abundance indices (WVI, NBC) and the Kope-Parken abundances (terminal + ocean fishery impacts), whereas they were not consistent between FRAM and the Kope-Parken metrics. FRAM “inland” abundances were positively correlated with SRKW fecundities (though not much better than a “no salmon” model), but were negatively correlated with SRKW survival rates. CTC abundances for WCVI and NBC were both strongly and positively correlated with survival rates, whereas fecundities were more weakly but positively correlated with these CTC indices. Kope-Parken abundance metrics (terminal runs, or terminal runs + ocean fishery catches) for various stock groupings (by ocean distribution patterns: north, central, south (California) or migration timing (spring, summer, summer/fall, fall)) were weakly but positively correlated with fecundities for the summer/fall stock grouping, and were strongly correlated with survival rates for both north and central ocean distribution groupings and for the fall stock grouping. Interestingly, the “top-rated” models, judged via AIC, usually excluded Fraser spring-run Chinook salmon and California Chinook salmon. Also spring and summer stock groupings (which produce fish with higher fat content than fall run stocks) were poor predictors of survival. These regression analyses seem generally consistent with a conclusion that SRKW vital rates are more highly correlated with broad scale aggregated abundances of Chinook salmon that share overlap in coastal geographic distribution with SRKW during early spring and late fall periods, and possibly also during the winter period. The Panel also notes that when SRKW forage for Chinook salmon during summer months in their critical habitat, they are taking advantage of high densities (fish per unit of water volume) of returning mature fish whereas foraging for Chinook salmon during other months in coastal waters must often mean that densities (fish per unit of water volume) of Chinook salmon are much lower than in the summer critical habitat. Together, these logistic regression results and observations concerning relative densities of Chinook salmon in different geographic areas and months suggest to the Panel that abundance of those specific Chinook salmon stocks that are present during the summer period and pass through the critical habitat of SRKW does not directly limit SRKW population growth. Instead, the Panel concludes that coastal abundance of Chinook salmon during non-summer months is probably more important for successful survival and reproduction of SRKW.

Mature vs. immature Chinook salmon

The use of the Kope-Parken terminal run size estimates as a metric in Ward's logistic regression analyses, and in some of the subsequent predictions of changes in SRKW population growth rates due to elimination of fisheries (Ward 2012), reflects a positive response to the Panel's conjecture that, at least during the summer period, SRKW must be intercepting and primarily consuming maturing/mature Chinook salmon en route to their freshwater spawning grounds. As noted above, however, it is conceivable, even perhaps likely, that abundance of Chinook salmon during winter months is more critical to successful reproduction and survival of SRKW. If so, then Ward's use of Kope-Parken's estimates of both terminal run size and terminal abundance + fishery catches as indicators of Chinook salmon abundance seems a worthy approach to address this key uncertainty.

Size Selectivity

The concerns expressed in the initial draft report by the Panel regarding the data used to fit age/size selection curves did not receive much attention at Workshops 2 or 3. There is no dispute from the Panel that SRKW appear to consume primarily larger and older Chinook salmon. Ford and Ellis presented scale-based observations showing that the mean age of kills (4.20 years) substantially exceeded the mean age of Chinook salmon estimated available off NE Vancouver Island (3.52 years); whale kills of age-5 fish were much greater than the relative abundance of age-5 fish, whereas whale kills of age-3 fish were much less than the relative abundance of age-3 fish (Ford and Ellis 2011). In some early-maturing Chinook salmon stocks, age-3 is often the dominant age at maturity. Therefore, maturation schedules of individual stocks could affect the degree to which abundance of individual stocks would convert to abundance of "suitably sized Chinook salmon" for SRKW in their summer critical habitat. This issue would also seem of importance for assessment of the abundance of Chinook salmon that might be effectively available to SRKW during winter months as ocean populations will consist of large fish only for those stocks which are not early-maturing (i.e., that would have large numbers of age-3 and older fish remaining in the ocean to mature at later ages).

Competing Risks of Death Framework

In the Panel's initial report following Workshop 1 (Hilborn et al. 2011), the Panel devoted considerable attention to concerns about the FRAM model structure, in particular with respect to how natural mortality (and predation on Chinook salmon by SRKW and NRKW) was treated, and the Panel suggested that a 'competing risks of death' framework might provide a more informative setting within which to model the effects of fisheries (and competing marine mammals) on potential consumption of Chinook salmon by killer whales. The Panel continues to feel that the competing risks of death framework may have considerable heuristic value for developing a better conceptual understanding of the joint dynamics of Chinook salmon predators (fishermen, SRKW, NRKW, harbor seals, sea lions) and their prey.

In its original draft report, the Panel showed that, under an assumption that killer whales consume an approximately constant number of Chinook salmon, the force of mortality (see **Appendix B**) associated with killer whales (and probably also the forces of mortality associated with other

pinniped predators), and the associated fraction of Chinook salmon abundance that is removed by these predators, likely increases dramatically as abundance of Chinook salmon decreases. In contrast, according to abundance-based management of Chinook salmon fisheries by the PSC, the expectation of death from fishing (exploitation rate) should be roughly constant at all levels of Chinook salmon abundance, though with small “jumps” at 0.5 and 1.0 levels of abundance indexes. These very basic observations suggest that “natural mortality” (predation from all non-human sources + all other natural causes of death) is quite unlikely to be independent of Chinook salmon abundance, as current models (like FRAM) assume. Furthermore, the probable effects of eliminating fishing as a cause of death, expressed as an increase in survival rate of Chinook salmon, must also surely change, perhaps dramatically, as Chinook salmon abundance changes. Given the potential rates of consumption of Chinook salmon by the SRKW generated by Ford et al. (2011) (67,000 – 81,000 Chinook salmon during the months of July and August, with range of from 342,000 – 410,000 Chinook salmon per year assuming 70% of diet is Chinook salmon), and conjecturing proportionally greater consumption of Chinook salmon by the NRKW, it is easy to imagine that the force of mortality associated with killer whales at low Chinook salmon abundance may be quite large, especially if Chinook salmon abundance consists only of a select group of populations that are actually available to SRKW and of appropriate size or age. The Panel did not intend, by advocacy of a competing risks of death framework, to suggest that current management models be changed to continuous models with forces of fishing and natural mortality operating simultaneously. Instead, the Panel meant to emphasize that competing risks of death provides a useful conceptual and quantitative framework within which to assess the effects of fisheries, as compared to those of other predators, on survival and abundance of Chinook salmon.

Preikshot and Perry (2012) presented Ecopath with Ecosim (EwE) modeling results that are related to the competing risks of death framework that the Panel recommended, although those results apparently reflect analyses originally carried out for another purpose within the context of a Strait of Georgia EwE modeling exercise. First, they noted that the force of fishing increased through the early 1980s, when it was perhaps 9-10 times the magnitude of the force of natural mortality on Chinook salmon, whereas during the period from 2000 to present, the force of fishing had become very much less than the force of natural mortality, which had itself approximately doubled (Preikshot and Perry 2012, slide 10). These changes presumably reflect the dramatic post-FCMA reductions in fishing and the corresponding rapid increase in pinniped abundance in this area. Preikshot and Perry (2012, slide 13) also suggested that simulated Chinook salmon mortality (force of mortality) in Georgia Strait associated with pinnipeds was well below that of killer whales for the period 1960-1985, whereas during the period 1990-2010 it was roughly comparable to that associated with killer whales. Although the Panel cannot judge the analytic merits of these results based only on what was presented in the workshop presentation, the pattern of increasing natural mortality for Chinook salmon does seem plausible. However, it is important to note that mortality rates in EwE are sensitive to the predator-prey interaction assumptions. Nevertheless, the EwE results suggest that exploring the consequences of a competing risks of death model for Chinook salmon, with SRKW, NRKW, harbor seals and sea lions all identified by unique forces of mortality, could provide important insights into probable temporal patterns of Chinook salmon mortality, the role that fishing has played in those patterns, and the likely consequences of removing ocean fishing as a cause of mortality on Chinook salmon.

In **Appendix B**, the Panel presents a preliminary illustration of the kinds of insights that might be generated from adoption of the competing risks of death (CRD) framework and provides some graphical illustrations of how forces of mortality and realized mortality rates of Chinook salmon associated with different causes of death (fishing, SRKW predation, NRKW predation, other non-fishing causes) may have varied over the past 25 years. In addition, **Appendix B** provides graphical illustrations of how forces of mortality associated with these different causes may vary as a function of ocean abundance of age-4 and age-5 Chinook salmon.

Among other things, the analyses presented in **Appendix B** suggest that:

- Natural mortality rates of Chinook salmon since the early 1990s have likely been substantially higher than has been assumed in current stock assessments for Chinook salmon;
- At the lowest levels of Chinook salmon ocean abundances that have been experienced over the 1979-2005 period (less than 2.5-3.0 million), the CRD model suggests that SRKW and NRKW exert much higher predation mortality, which could lead to annual Chinook salmon survival rates below 40% under low consumption or below 30% under high per-whale consumption scenarios;
- When Chinook salmon ocean abundance is greater than about 3.5 million, it appears that assumptions about natural survival rates of 80-90% are not unreasonable because mortality rates caused by killer whales would then be relatively low; and,
- One hypothesis emerging from the calculations is that NRKW may exert as much, or more, influence on SRKW growth rate as fisheries due to their large consumption of Chinook salmon.

2) Are the methods employed to predict salmon abundance by stock in specific times/places scientifically valid?

As LaVoy (2012) pointed out, only the FRAM model makes any attempt to model the seasonal abundance of Chinook salmon in specific times and places. The CTC model and the Kope-Parken run reconstruction estimates of total abundance (terminal runs + pre-terminal catches) are probably best thought of as projected pre-season abundances, prior to the beginning of the annual fishery cycle. The Kope-Parken stock-specific terminal run sizes, coupled with knowledge of run timing of stocks could, however, be used as excellent descriptors of abundance in near terminal locations and might be easily modified under various assumptions that might concern levels of fishing.

The Panel's understanding is that the FRAM seasonal abundances for various stocks are based on CWT recovery data from the late 1970s when ocean fisheries were much less restricted than current fisheries so that it was reasonable to conclude that the ocean catch distribution of CWTs from a given stock probably provided a reasonable picture of a stock's changing geographic distribution through time. Contemporary fisheries, which have extensive time/area closures, would not provide useful information on ocean distribution patterns based on CWT recoveries. Whether or not the "historic" (late 1970s) ocean distribution patterns for various stocks can be reasonably assumed to apply to contemporary management is an open question that has in part motivated on-

going fishery-independent GSI-based surveys of salmon off Oregon and California (e.g., Goldenberg and Fitzpatrick 2011).

For many stocks, existing CWT recovery data provide a moderately good basis from which to judge whether or not certain stocks would likely be found within the poorly understood SRKW winter “range”. For example, Ford et al. (2012) expressed belief that it would be unlikely for stocks of Chinook salmon north of south central British Columbia to be found within the winter range of SRKW. Also, as noted previously, California (Sacramento, Klamath) and southern Oregon (Rogue) Chinook salmon stocks would be available in large numbers only during those years when SRKW spent considerable time off the Oregon and California coasts.

3) Are there improvements to the methods you would suggest?

Given the possibility that the availability of Chinook salmon to SRKW may be more important during the non-summer months, including winter, it seems important to develop improved fishery-independent assessments of current Chinook salmon distribution patterns (e.g., Goldenberg and Fitzpatrick 2011) during spring through fall months and to also somehow develop a better notion of winter distribution of Chinook salmon stocks. As ocean Chinook fisheries have been more restricted in time and space, our understanding of ocean Chinook distribution has become more limited. The paucity of winter fisheries and thus samples for CWT or genetic analysis means our understanding of winter distribution is particularly limited.

As noted above, it would seem appropriate to explore the implications of competing risks of death approaches to assessing impacts of predation by marine mammals and fishermen on Chinook salmon and to thereby gain improved insight concerning the potential impacts of changes in fisheries on availability of Chinook salmon to SRKW.

4) Are the methods employed to predict the reduction in salmon abundance by stock in specific times/places scientifically valid?

The Panel interprets the intention of this question as trying to get at the reliability with which statements could be made concerning the potential increase in abundance of Chinook salmon that might result if ocean fisheries (and possibly also freshwater fisheries) were modified or eliminated.

Methods presented in workshops seem appropriate to assess the short-term impacts that reductions of fishing might have on ocean and terminal abundances of individual stocks of Chinook salmon. Based on a review of CTC model-based calculations of ocean fishery exploitation rates for the various CTC stock aggregates (provided by Kope), it appears that the average ocean fishery exploitation rates for age-3 and age-4 fish in the past several years have been about 0.15 - 0.20⁶. Using accounting models such as FRAM, these exploitation rates, if reduced to zero, would be expected to increase ocean abundance and terminal run sizes of Chinook salmon from perhaps 18%

⁶ The Panel made no attempt to carefully average age-specific exploitation rates across stock aggregates and would not know how to do so in an appropriate fashion, but the Panel does wish to state its recognition that there is substantial variability in exploitation rates among stock aggregates.

(0.15/0.85) to 25% (0.20/0.80) *if fishing were the only source of mortality*. Recognizing that there are other forces of mortality on Chinook salmon, including possibly quite large forces of mortality associated with marine mammals, the Panel believes that a 20% increase represents an upper limit to short-term abundance increase due to reduction in fisheries and that such an increase would be much more modest when Chinook salmon were at low abundance levels. Chinook salmon ocean abundance increases projected in workshop presentations were a bit less than 20% for non-Puget Sound stocks, and much lower for Puget Sound stocks (which presumably now have much lower exploitation rates), but fairly comparable to guesses that might be made based on examination of age-3 and age-4 ocean fishery exploitation rates.

Such short-term (annual) changes in ocean abundance and terminal runs of Chinook salmon need to be distinguished from possible multi-year and longer-term improvements in ocean abundance of Chinook salmon that could theoretically be achieved via manipulation of exploitation rates in ocean and/or freshwater fisheries. Such long-term changes in ocean abundance of Chinook salmon seem worthy of more attention than they have thus far received (see Section 4.4 below).

4.4 Effects of Possible Reductions in Fisheries on Abundance of Chinook Salmon

Based on material presented at the workshops and on analyses made by Panel members, the Panel developed a summary of anticipated impacts that reduction and/or changes in Chinook salmon fisheries could have on abundance of Chinook salmon. Among other things, the Panel believes: 1) that it is important to distinguish short-term effects from long-term effects that might result from changing fishing regimes; 2) that it is important to recognize that fishing regimes could be changed in both terminal (freshwater fisheries and marine fisheries focused on maturing fish) and ocean fisheries; and 3) that it is important to acknowledge that effects of changes in fishing would be different for hatchery stocks than for wild stocks. The Panel summarizes these anticipated impacts in the bulleted list provided below.

For wild populations:

Short-term/annual accounting:

- If "all ocean fisheries were closed", there would be a short-term increase in ocean abundance of Chinook salmon available to SRKW due to the direct reduction in ocean fishing. This effect would probably be a maximum of about 25% from an annual accounting perspective.
- Elimination of all ocean and terminal fisheries would have an identical short-term effect on ocean abundance of Chinook salmon as given in previous bullet because freshwater fisheries reduce Chinook salmon abundance only after killer whales (and other marine mammals) have had an opportunity to intercept them. Therefore, freshwater fishery reductions could only contribute to long-term changes in Chinook salmon abundance via their impacts on spawning stock abundances.

Long-term accounting:

- Assuming that Ricker stock-recruitment models are appropriate for most Chinook salmon stocks, fisheries could be managed for maximum recruitment rather than maximum yield, thereby increasing recruitment via an increase in spawners.
- Long-term achievement of maximum recruitment under a Ricker model would require some harvest to be allocated across marine and freshwater fisheries so as to achieve a harvest rate (expressed in terms of adult equivalents) that would maximize recruitment. (Total recruitment is anticipated to be less under a no-fishing scenario than with some fishing.)
- Maximum ocean abundance of Chinook salmon available to killer whales would be achieved with harvest taking place only in freshwater, with freshwater fisheries set to reduce spawning stock so as to achieve maximum recruitment.
- Assuming that fisheries are currently managed to allow Chinook salmon escapements near their MSY levels, shifting to management for maximum recruitment might increase ocean recruitment by about 6-9%, based on stock-recruitment relationships currently used by CTC.
- If ocean fisheries were eliminated and freshwater fisheries were managed for maximum recruitment, then there would be an additional benefit, compared to the present, due to elimination of ocean interception of immature salmon prior to maturity. For a given stock, this benefit would depend on the current age-specific ocean fishery exploitation rates and the stock-specific maturation schedule. For most stocks, this benefit would typically probably be at least an additional 20% above the benefit due to increased recruitment.
- If ocean fisheries and freshwater fisheries were both eliminated, the long-term effect, assuming a Ricker model, would likely be reduced recruitment as compared to the present, although possibly with some benefits to ocean abundance, again through elimination of interception of immature fish. The logic of this statement is based on an assumption that the natural equilibrium recruitment (expressed as adult equivalents) falls to the right of the dome of the Ricker model, the usual case.

For hatchery populations:

- Because existing fisheries rarely prevent hatchery returns from achieving the numbers required to meet hatchery production goals, recruitment of hatchery fish can safely be assumed independent of fishery regimes.
- If ocean fishing were eliminated, ocean abundance of hatchery fish would be increased via elimination of immature fish that would otherwise remain in the ocean. For a given stock, this benefit would depend on the current age-specific ocean fishery exploitation rates and the stock-specific maturation schedule. This benefit would typically be at least an additional 20%. Elimination of freshwater fisheries would have no effect on ocean abundance of hatchery stocks and would therefore generate no benefits in terms of availability of hatchery fish to SRKW.

In summary, maximum long-term increases in abundance of Chinook salmon that might theoretically be available to SRKW would be achieved by eliminating all ocean fishing (typically at least 20% increase in ocean abundance of age-4 and age-5 hatchery and wild fish due to elimination of ocean fishery interception of immature fish) and by maximizing recruitment through manipulation of freshwater exploitation rates to maximize recruitment (6-9% increase in recruitments of wild fish; no impact on hatchery fish).

4.5 Recommended Information and Analyses

- Further analysis of all available information that might shed light on winter distribution of Chinook salmon stocks and SRKW, including attempts to “weight” observed spatial distributions of SRKW according to sampling levels and locations at which acoustic receivers have been deployed (e.g., deployment of acoustic receivers off the Washington coast seems much greater than off the California coast and must affect detection probabilities).
- Develop improved measures of the abundance of harbor seals and sea lions, as well as their predation impacts on Chinook salmon.
- Continue to evaluate the possible influence of abundance of competing marine mammals (NRKW, harbor seals, sea lions), as well as seasonally available alternate chum salmon prey, on fecundity and survival rates of SRKW and NRKW.
- Explore the competing risks of death (CRD) framework (Quinn and Deriso 1999) as a simple, heuristic approach to investigating interactions among competing predators, in the context of potential expected benefits to SRKW due to reduction/elimination of fishing at different relative abundances of Chinook salmon. The CRD approach could help to integrate broader ecological understanding into mechanistic models of the Chinook salmon–Marine Mammals–Fisheries system since all of these dynamics are intertwined. (See **Appendix B.**)

5.0 PROJECTED FUTURE STATUS AND RECOVERY

5.1 Context

The Panel was asked to evaluate the available information and analyses concerning projected future population status of SRKW and how Chinook salmon fisheries might affect such status. In addition, the Panel evaluated existing indicators for measuring recovery of SRKW against US and Canadian endangered species criteria. The Panel was also asked to address the most fundamental and contentious issue involved in evaluating Chinook salmon fishery effects on future status and recovery—namely whether existing correlative evidence for past linkages between SRKW vital rates and indices of Chinook salmon abundance meets the necessary criteria to imply causality between future Chinook salmon abundance and future SRKW status.

Key Question 1 focused on the past by asking that the Panel examine the methods used to establish historical relationships between salmon abundance and killer whale survival and birth rates. Other sections of this report review SRKW population growth rates, the biological justification for linking salmon to SRKW nutritional status, and fishery effects on salmon available to SRKW. Therefore, the Panel looked specifically at how this historical information has been used to estimate population model parameters for salmon effects on SRKW dynamics, as well as the basis for attributing causation to correlative evidence. Key Question 2 focused on the future by asking the Panel to review the basis for forward projection models used to assess future status and recovery of SRKW under alternative salmon abundance scenarios. Projecting SRKW abundance forward in time, although technically feasible, involves a suite of assumptions and is, therefore, far more uncertain than fitting those models to past abundance data. Therefore, the Panel provides a critical review of the assumptions and conditions behind those projection model components.

Key Question 1. Are the methods employed to evaluate the relationship between salmon abundance and SRKW (and/or NRKW) fecundity, survival and population growth scientifically reasonable? Do you have any additional analyses or specific suggestions to improve the methods?

The Panel considers the methods used to evaluate the relationship between salmon abundance and killer whale fecundity, survival, and population growth rates scientifically reasonable and, in several respects, state-of-the-art. The quantitative evaluation, which mainly took the form of Bayesian logistic regression modeling of age-/stage-structured survival and fecundity data, encompassed a wide range of covariates, including salmon, marine mammals, and climatic factors. In practically all cases, there were reasonable hypotheses for including various factors, although these were less clear when it came to Chinook salmon variables. For instance, some Chinook salmon indices used in the regression analyses contained stocks that may not be readily available to SRKW. Nevertheless, results of the correlative approaches (Ward et al. 2009, Ford et al. 2010a), as well as additional presentations at Workshops 1-3 linking Chinook salmon abundance to SRKW vital rates were reasonably consistent with expected dynamics of a highly selective predator and its primary prey.

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A large body of supporting data and analyses were presented to support a plausible mechanistic link between SRKW vital rates and broad-scale indices of Chinook salmon abundance. Perhaps the strongest data are the May–September feeding, diet, and social structure observations of resident killer whales (Ford et al. 2009, Hanson et al. 2010a, Ford and Ellis 2011, Hanson 2011, Ford 2012a). Although the details of these processes are uncertain outside the summer period, information presented in Workshop 3 supported the notion that overlap is possible between SRKW and most Chinook salmon stocks with origins south of central British Columbia in any season, including winter (Weitkamp 2010, Ford et al. 2012). Stable isotope and contaminant load (O'Neill et al. 2012a, 2012b) analyses were also consistent with an SRKW diet comprised of Chinook salmon from a wide range of sources well outside the narrowly defined Puget Sound/Fraser River area.

Correlation-Causation Debate: Although there is a reasonable body of scientific evidence showing that Chinook salmon are important prey for SRKW, there is a limited range of specific observational evidence and no possibility of experimental evidence linking Chinook salmon abundance to SRKW population growth. Because SRKW growth and salmon abundance data are observations of uncontrolled events obtained from an unknown sampling design, there is a high risk of incorrectly assigning causes to correlations and making relatively weak inferences. Ultimately, the existing information is most effective for hypothesis generation (Schwarz 1998).

Workshop 3 provided an opportunity for several participants to debate the correlation vs. causation issue from a weight-of-evidence perspective (Burkhardt-Holm and Scheurer 2007). Causation in this instance is specifically meant to imply that observed changes in Chinook salmon abundance have been a primary cause of the observed changes in SRKW population growth rates. The panelists were given three questions, two of which were:

- 1) What is the strength of evidence that changes in Chinook salmon abundance cause or do not cause changes in SRKW vital rates?
- 2) What is the strength of evidence that changes in fisheries in the future would cause or would not cause changes in Chinook salmon abundance sufficient to affect SRKW vital rates?

Not surprisingly, none of the 5 responses provided specific and unequivocal answers to these questions. For question (1), responses varied from broad lists of evidence in favor of a cause, to rather specific evidence suggesting that cause should be rejected for all except one particular Chinook salmon abundance index. Other panelists remained "unconvinced" given the possibility of alternative ecosystem-level mechanisms or thresholds dividing Chinook salmon abundance into low levels where causation seems likely to high abundance where causation seems unlikely. At least two panelists suggested that any causal effects arising from (2) would probably be weak, given the estimated effect sizes from statistical modeling. One panelist suggested that changes in future fisheries should only be considered for fisheries harvesting Chinook salmon stocks for which a causal relationship to SRKW vital rates has not been rejected based on statistical significance of a relationship and meaningful overlap between abundance and SRKW ranges. Several panelists also pointed out that the impacts on SRKW of changes to Chinook salmon fisheries would need to

consider how an increase in available salmon might be spread across salmon predators (e.g., SRKW, NRKW, pinnipeds).

5.2 Forecasts of SRKW Future Status

In the original Biological Opinion on the Puget Sound Chinook Harvest Management Plan, NOAA Fisheries devised and evaluated alternative fishery regimes to assess their relative impact on future status and recovery of SRKW (NOAA/DFO letter to Panel). Over the course of three workshops, the alternative fishery regimes have essentially been reduced to two: (1) maintain status quo with annual ocean fishery exploitation rates on the order of 20% and (2) close all ocean fisheries. Such a simplification is probably warranted in this case given what appears to be a revised understanding of interactions between fisheries and SRKW. In particular, it seems to be a gross extrapolation to implicate any particular fishery, including those during the peak Chinook salmon abundance period in summer, in affecting SRKW population growth rate. Instead, a more plausible working hypothesis is that highly mobile SRKW (and NRKW) respond to larger spatial scale changes in Chinook salmon abundance than can be appreciably affected by any specific Chinook salmon fishery.

With the alternative fishery scenarios as defined above, and a working hypothesis, we now turn to addressing one of the original questions posed in this section (i.e., **Key Question 3**).

Key Question 3: Based on your expert opinion, what level of confidence would you assign to the conclusion that predicted changes in Chinook salmon abundance caused by fisheries affect the population growth rate of the SRKW?

Clearly, all of the issues and concerns raised in the correlation vs. causation debate apply here to Key Question 3. To state the Panel's opinion, the evidence seems reasonably strong that vital rates of SRKW are, to some degree, ultimately affected by broad-scale changes in their primary Chinook salmon prey. However, even if there is a causal mechanism, the Panel's opinion is also that such a mechanism is probably not a simple linear cause-and-effect one for a variety of reasons. For example, if Chinook salmon abundance is causally related to SRKW mortality and fecundity, then it also seems likely that SRKW (and other predators) can cause changes in Chinook salmon mortality (see **Appendix B**). Such feedbacks imply non-linear density dependence in SRKW growth rate (e.g., a large region of Chinook salmon abundance over which growth response is small, but a small region where growth response is large). The logistic regression models and supporting auxiliary evidence reflect only a narrow range of abundance for both SRKW predators and their Chinook salmon prey, which increases the risk of poorly capturing these relationships. Thus, the Panel's overall view is that the predator-prey system involving Chinook salmon, SRKW, NRKW, and some pinnipeds is only partially described by correlations between Chinook salmon and SRKW. Therefore, any predictions about impacts of changing fisheries may not be robust to changes in the status of other Chinook salmon predators, or even to changes in Chinook salmon abundance.

Confidence in conclusion for Key Question 3: Low.

Justification for the Panel's low degree of confidence in the conclusion stated in Key Question 3 is based on arguments for or against the two underlying premises.

(1) Models for predicting the future distribution of Chinook salmon abundance accurately capture the dynamical response of future Chinook salmon abundance to fishery closure (i.e., eliminating a 20% ocean exploitation rate).

Current models used to predict future salmon abundance assume that Chinook salmon mortality components are independent and strictly additive, and production follows a density-independent random-walk process. The former are typical assumptions used in single-species fisheries models, including FRAM and CTC models that form the basis for Chinook salmon abundance modeling, while the latter assumes independence between Chinook salmon abundance and predator abundance, as well as lack of Chinook salmon recruitment response to changes in spawning abundance (i.e., if spawning abundance actually increased in the absence of fishery exploitation). If all of these assumptions hold, then removing the fishery would cause a 25% increase or more (see Section 4.0) in available Chinook salmon abundance across all stocks.

Alternative assumptions could be used in predicting future Chinook salmon abundance. For example, Chinook salmon mortality components are not independent and not strictly additive (i.e., multiple competing predators), and production follows density-dependent processes (e.g., Ricker) with ocean survival depending on predation regime. These are typical assumptions used in multi-species fisheries and trophic models (e.g., Ecosim; Preikshot and Perry 2012), as well as predator-prey models, for example involving ungulates, wolves, and large cats. Removing a 20% fishery exploitation rate would have short- and long-term effects as well as differential effects by stock via stock-specific density-dependence (see Section 4.0). In the short-term, maximum Chinook salmon abundance change would be +25% assuming that all fishing and predation impacts are independent and additive (see **Appendix B** and Section 4.0). Long-term changes in Chinook salmon abundance would be dependent on interactions between abundance, ocean predation and freshwater density-dependent production (Section 4.0). This suite of alternative assumptions is probably more "realistic", but also more difficult to quantify and assess from existing data than the current set of assumptions used to model future Chinook salmon abundance.

(2) Changes in Chinook salmon abundance caused by fisheries affect the population growth rate of the SRKW.

The implied causality within this premise has already been discussed above. Suppose for the sake of the present argument that we allow for a causal relationship between Chinook salmon abundance and SRKW growth rate. The approach used to fit a SRKW population dynamics model to observed births, survival, and salmon data has also been discussed already and given reasonably strong endorsement by the Panel as a scientifically reasonable means of parameterizing a SRKW population projection model. A central issue involved in earlier reports and discussions with the Panel focused on the process error variance represented in this projection model. The term "process error" in this context means uncertainty or unexplained variation in the data resulting from the choice of model boundaries. Distributions of these process error effects are usually assumed known and range from simple binomial variation in survival rates and sex ratios at-birth

to perhaps auto-correlated random-walk processes influencing birth rates. The error variance of the logistic regression models linking Chinook salmon abundance to SRKW growth rates is used to capture the missing process error effects of unmodeled factors. For example, **Figure 5-1** shows that the posterior predictive distribution for SRKW birth rates effectively captures both the long-term pattern and range of the observed births. Similar distributions would apply to sex ratio at birth and survival rates. Therefore, the random process errors in projections of future SRKW population size should produce a distribution of future SRKW population size trajectories that is highly likely to contain the true future trajectory.

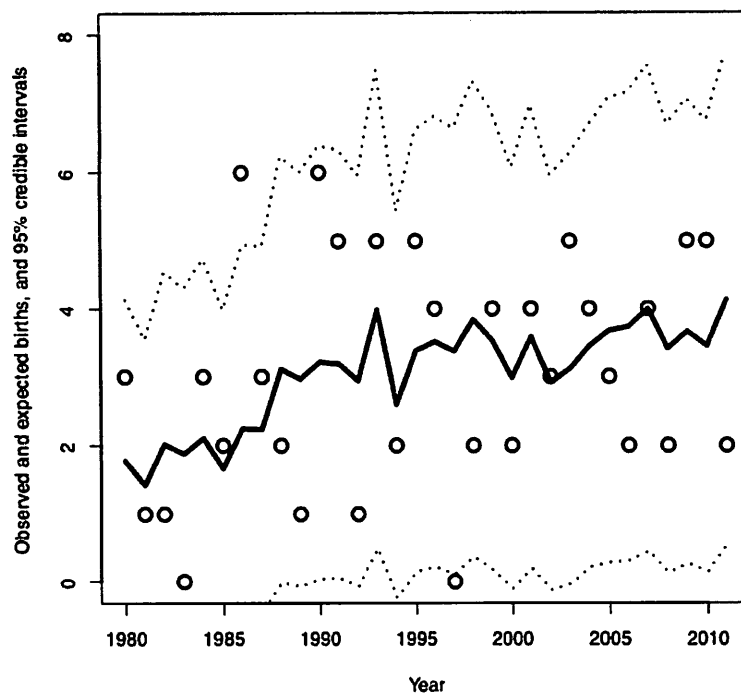


Figure 5-1. Posterior predictive distribution and observed births for SRKW. The solid line is the mean of the distribution and the upper and lower dotted lines are the 0.975 and 0.025 quantiles, respectively. The circles are observed births. Revision of original source: (Ward et al. 2009).

Process errors actually influence future population dynamics via multiple feedbacks, so assumptions about their structure may be critical to the robustness of future SRKW projections regardless of whether the SRKW growth rate is causally linked to Chinook salmon abundance or just correlated. In essence, process errors arising from unmodeled factors propagate (i.e., compound) via the population dynamics model and rather rapidly lead to a lack of robustness of model predictions if their structure is incorrect. Even though conclusions are correctly drawn from the distribution of future population trajectories, the timing and probability of specific events described by these distributions (e.g., probability of meeting delisting criteria within 28 years) will not be robust.

The Panel, as well as workshop presentations and supporting literature, highlighted numerous unmodeled factors and processes that may not vary in simplified random ways. Primary attention

has been given to the presence and dynamics of alternative Chinook salmon predators, relatively stable consumption requirements of long-lived mammals, mobilization of killer whale body contaminant loads, feeding and social behavior, etc.

The alternative fishery regimes represent a rather small change of exploitation rate and the models used to predict the future impact of this change are only reliable under rather restrictive dynamic model assumptions and state conditions (e.g., low Chinook salmon abundance, high SRKW abundance). Attaching a suite of caveats to a predicted small effect size should only result in relatively low confidence in the predictions.

5.3 Recovery criteria

The Panel was specifically asked to comment on "(e) scientific considerations relevant to potential performance criteria for determining risk to SRKW from fisheries impacts" (NMFS 2011a). Presentations in Workshops 1-2 (Barre 2011, 2012), as well as letters to the Panel, further emphasized the need to "provide advice on the utility of PBR, and any other suggestions for performance criteria and metrics for evaluating the effects of actions on SRKW"[Panel paraphrasing].

It is important to note that criteria aimed at measuring recovery success differ between the US and Canadian contexts. Although the Panel was not asked to comment on recovery criteria under the Canadian recovery strategy for SRKW, they are presented here as a complementary perspective (**Box 5-1**). In general, note that Canadian recovery performance metrics are more qualitative than quantitative in that they do not specify specific numerical targets or thresholds for abundance or population growth rates, both of which were key topics debated in the workshop process as well as within this report.

Box 5-1. Interim Measures of Recovery Success for SRKW Recovery Strategy
(Fisheries and Oceans Canada 2011).

- a) Long-term maintenance of a steady or increasing size for populations currently at known historic maximum levels and an increasing size for populations' currently below known historic maximum levels;
- b) Maintenance of sufficient numbers of females in the population to ensure that their combined reproductive potential is at replacement levels for populations at known historic maximum levels and above replacement levels for populations below known historic maximum levels;
- c) Maintenance of sufficient numbers of males in the population to ensure that breeding females have access to multiple potential mates outside of their own and closely related matriline;
- d) Maintenance of matriline comprised of multiple generations to ensure continuity in the transmission of cultural information affecting survival.

General Comments

Assessing the status of a population requires unambiguous and measurable recovery criteria that are to be compared against objectives. The standard approach to developing such criteria is to word them in such a way that a group of knowledgeable people, given a description of the issue, could agree in the future whether or not a particular criterion had been met (Morgan and Henrion 1990). This so-called "clarity test" further implies that any quantities included in the criteria must also be measurable, possessing real true values, and be repeatable such that the same information would lead to the same conclusions. Repeatability further implies that the methods used to compute the criteria are clearly defined. Developing measurable population recovery criteria should therefore include definitions for:

- 1) Population characteristics that can be reliably and repeatably measured or inferred (e.g., abundance, growth rate, age-structure, sex ratio);
- 2) Thresholds and/or target values for these characteristics that uniquely define population status (e.g., "recovered", "depleted");
- 3) Probability level at which the measured population characteristic is said to meet the target (or exceed the threshold);
- 4) Temporal (or spatial) frame over which to measure the characteristic and probability; and
- 5) A clear method for calculating the specified population metrics.

In reviewing the Biological Opinion (NMFS 2011a), recovery plan (NMFS 2008), 5 Year Review (NMFS 2011b), and the Canadian recovery strategy (Fisheries and Oceans Canada 2011), the Panel was not able to identify any threat, status, or recovery criteria defined explicitly in terms (1)-(5). In particular, the *Threats Criteria* described in the 5 Year Review do not seem to have clearly defined conditions upon which the threat criteria could be met. There is clearly a considerable amount of research activity aimed at studying the threats, but without explicitly defined and measurable objectives, it is difficult to determine how the research will contribute to removing the threats.

Performance Criteria for Assessing Recovery

Population growth rate: Population growth rate would seem, at first thought, to be reasonably straightforward to measure and apply as a recovery criterion, especially for SRKW because observation error in abundance is very low. However, as demonstrated in the workshop process, the methods used to define and estimate population growth rate must be made more explicit because the calculations involve assumptions about the underlying population dynamics model as well as the time frame over which the rate is measured. Even the most basic population trend estimator (i.e., that follows the basic laws of population growth), assumes a time frame ($t - k$) and an exponential population growth model of the form $N_t = N_{t-k} e^{\lambda(t-k)}$, where λ is the population growth rate. An estimate of λ is then obtained via ordinary linear regression between logarithms of population size and year t (i.e., linearize the growth model to $\log N_t = \log N_{t-k} + \lambda(t - k)$).

Incorporating the important effects of population age- or stage-structure on growth rate requires disaggregating abundance into multiple age or stage classes, and also disaggregating the population growth rate into distinct survival and reproduction components for each class. However, even though such expansion of assumptions underlying the population growth rate estimate is well-supported by the available data, as demonstrated in Workshop 3, alternative methods for computing stage-specific survival and fecundity rates can lead to very different results (see Section 2.0).

The ability of population growth rate to indicate status or recovery depends on the particular situation in which it is applied. Basic population dynamics theory dictates that the population growth rate cannot remain constant over too wide a range in population size and must eventually decline to zero at some non-zero value of population size. Growth rate estimates for the whole SRKW population, as well as pod-specific values (Section 2.0) suggest that the total population is growing slowly, while J and K pods are growing faster than L pod (although they are also smaller). It is still not clear whether these low growth rates are to be expected because the total population is near carrying capacity of 100-150 whales, or whether they are unexpectedly low for a population far from its carrying capacity of ~400 whales. Since a population's growth rate will decline as it nears carrying capacity, a growth rate recovery criterion is intrinsically problematic. An approximate doubling of the NRKW population over the past 30 years suggests that the conditions for this SRKW neighbor population were good enough to support sustained growth where possible.

The growth rate criterion used to assess recovery of SRKW includes three of the five required elements for a measurable objective. It is missing a probability level of achieving the 2.3% rate, and specification of the method used to calculate the growth rate. The strength of quantitative

assessments of historic population growth rate as presented to the Panel is in the posterior distribution of λ , which can be used to provide the required probability that the population growth rate exceeds 2.3%. The posterior distribution of λ showed some weight of evidence in the right tail of growth rates where $\lambda > 1.023$, indicating that historic rates exceeding recovery criteria cannot be ruled out. At the same time, there is complementary evidence in the left tail indicating that historic growth rates were negative (i.e., $\lambda < 1.0$). There is no reference in the supporting material to a $\lambda < 1.0$ status or recovery criterion, so the Panel cannot comment on the non-trivial probability ($p \sim 0.07$) that the population growth rate is negative. Choosing a probability criterion is definitely not straightforward because it defines the allowable risk that, for example, SRKW decline in the future without an attempt at mitigation.

Population abundance: The attraction of abundance-based metrics, especially for SRKW, is the high accuracy and precision with which abundance of the majority of the population is measured. The number of individuals in small populations also features prominently in status criteria defined by US, Canadian and IUCN conservation guidelines. In Canada, small population size (i.e., $N < 250$) is the main criterion for which SRKW are listed under SARA. Because the condition for listing is also the condition for delisting, it seems likely that SRKW will remain listed under SARA for the foreseeable future.

Using abundance-based recovery criteria to downlist SRKW under the US ESA requires choosing a target abundance level amidst considerable uncertainty in the historical population size. For example, the Biological Opinion (NMFS 2011a, p. 42) states:

"The historical abundance of Southern Resident killer whales is estimated from 140 to an unknown upper bound. The minimum estimate (~140) is the number of whales killed or removed for public display in the 1960s and 1970s added to the remaining population at the time the captures ended. Several lines of evidence (i.e., known kills and removals [Olesiuk et al. 1990], salmon declines [Krahn et al. 2002] and genetics [Krahn et al. 2002, Ford et al. in press]) all indicate that the population used to be a lot larger than it is now, but there is currently no reliable estimate of the upper bound of the historical population size. When faced with developing a population viability analysis for this population, NMFS' biological review team found it reasonable to assume an upper bound of as high as 400 whales to estimate carrying capacity (Krahn et al. 2004)."

It appears that an abundance recovery target of 140 animals has a reasonably sound empirical basis, while the upper bound of 400 is somewhat arbitrary. The Panel could not find any further justification for 400 animals in the SRKW population, except from population genetics studies (Ford and Parsons 2012), although those are uncertain as well. As discussed below for extinction risk projections, choosing an upper bound of 400 may lead to an under-estimation of extinction risk if the actual carrying capacity is much smaller.

Note that recovery strategies for resident killer whales in Canada do not use abundance as a recovery target, mainly because of difficulty establishing historical population sizes (Fisheries and Oceans Canada 2011).

Projected changes in abundance: As mentioned above, abundance has the attractive feature of measurability, which allows for direct monitoring of progress against recovery goals. If instead, recovery goals are based on projections of abundance, say one or two generations into the future, then several uncertainties creep into the problem. First and foremost, the projection model scenarios chosen to establish recovery potential and metrics have a strong influence on perceptions about the efficacy of alternative recovery strategies. The Panel's low confidence in the future predictions of Chinook salmon abundance and SRKW responses to that abundance (see above response to **Key Question 3**) is essentially repeated here. This is not meant to imply that the population modeling is not a valuable and worthwhile research activity. On the contrary, the Panel believes that the models should be refined and used to make *a priori* predictions for future SRKW dynamics that can then be compared to observations in the normal process of scientific investigation. The Panel's point is that these models are simply not mature enough at this time to warrant a high degree of confidence in their predictions alone.

Projected changes in extinction risk: Recovery criteria based on extinction risk are sensitive to several factors, including *inter alia*: (1) variation in the specific definition of extinction and (2) the difficulties involved in modeling future SRKW abundance as discussed above, as well as choices for population viability analysis (PVA) scenarios. According to SRKW recovery plans, "NMFS defined 'quasi-extinction' as the stage at which 10 or fewer males or females remained a threshold from which the population was not expected to recover" (NMFS 2008). In Workshop 2, quasi-extinction was taken to be $N < 20$ individuals (Ward 2012). Although quasi-extinction is, by definition, a somewhat arbitrary choice, the specific criteria for SRKW should at least be consistent among PVA analyses.

Earlier assessments of extinction risk (e.g., Krahn et al. 2004) found that such risks are strongly dependent on SRKW carrying capacity and catastrophic effects assumptions (i.e., the two factors for which there is the least amount of data or experience). For instance, absent a catastrophe and given the observed range of survival and fecundity over the past 29 years, quasi-extinction risk for SRKW over 300 years increases 10-fold as carrying capacity values decrease from 400 down to 100 whales (Scenario A(Q)1 in Krahn et al. 2004). Higher carrying capacity implies greater scope for population growth at current abundances (~87 whales) and thus rapid growth away from quasi-extinction thresholds, while lower carrying capacity implies little scope for growth away from quasi-extinction thresholds.

There have been catastrophic losses of killer whale populations in the past, although the rarity with which they occur makes it difficult to assign probabilities of occurrence. For example, the following quote describes killer whale population declines associated with the 1989 Exxon Valdez oil spill in Prince William Sound, AK (Matkin et al. 2008):

"The loss of 33% of AB Pod and 41% of the AT1 Group from the time of the spill through the following winter of 1989–1990 is a catastrophic event with no precedent in any population of killer whales in the North Pacific (Ford et al. 1998, 2000, Matkin et al. 1999a) and is well outside the normal range observed in other pods from the southern Alaska resident population."

Although the threat of an oil spill features prominently in the SRKW 5-year status review (NMFS 2011b), there was no mention in the actual modeling work in NMFS (2011) or Krahn et al. (2004) of the impact of the Exxon Valdez oil spill on killer whale populations in Alaska. This suggests that the original PVA models could have under-represented the magnitude of catastrophic effects from events like oil spills. In addition, the PVA did not contemplate persistent effects of a single catastrophe, even though the effects of the Exxon Valdez spill appear to have persisted for more than a decade (Peterson et al. 2003, Matkin et al. 2008).

Key Question 2. Are the methods employed to evaluate the viability of the SRKW under alternative assumptions about future salmon abundance scientifically reasonable? Do you have any specific suggestions to improve the methods?

The PVA methods used for SRKW recovery planning are as scientifically reasonable as any other application of these methods. See below for suggested ways to improve them.

Key Question 5. Based on your expert opinion, what level of confidence would you assign to the conclusion that predicted changes in Chinook salmon abundance caused by fisheries increases the risk of extinction of the SRKW population?

The Panel assigns very low confidence that future fisheries will appreciably affect the extinction risk of SRKW. Besides great uncertainty in the actual extinction risk caused by unmodeled, yet plausible process effects (i.e., of salmon and SRKW dynamics), the effects of fisheries in existing PVA models are much smaller than effects of carrying capacity and catastrophic mortality events.

Ratios of prey available to prey required: Prey availability, measured one way as the ratio of prey available to prey requirements given metabolic demands associated with SRKW abundance and population structure, is an attractive performance metric for recovery strategies because these are potentially controllable by decision-makers. Analyses presented in the workshops (Noren 2011b, 2012) as well as recent published studies (Williams et al. 2011) suggest that Chinook salmon requirements for a SRKW population of 87 animals (and assuming current population structure) range from 211-364,000 age-4 equivalents per year. These estimates are clearly valuable pieces of information to consider given the specialist predator-prey relationship between SRKW and Chinook salmon.

The challenge in using these ratios will obviously be in determining what salmon are available given fluctuations in Chinook salmon abundance as well as competition with other salmon predators. The example competing risks of death framework in (**Appendix B**) shows one way to evaluate how available prey changes with changes in the abundance and prey requirements of competitors, as well as how the relative force of mortality is partitioned among various predators and fisheries.

Potential biological removal (PBR): As part of Workshop 1, the Panel was asked to comment on the following in relation to PBR,

"If the effects of prey reduction on killer whale population dynamics due to a specific action were quantified in a manner similar to the effects of a direct

harvest or harvest bycatch action, would using a bycatch-oriented framework such as PBR be a reasonable approach for assessing these effects?” (Barre 2012)

PBR is not specifically a recovery criterion, but rather an operational procedure for setting the allowable level of impact to a population depending on its status. This level of impact, or allowable removal, is based on the formula,

$$PBR = N_{\min} \frac{R_{\max}}{2} F_R$$

which is just the harvesting equation for a logistic growth model in which N_{\min} (87 for SRKW) is the minimum population size estimate, R_{\max} is the maximum rate of growth (assumed 0.04 for SRKW), and F_R is a safety factor used to reduce allowable removals as per Marine Mammal Protection Act guidelines for endangered ($F_R=0.1$), threatened or depleted ($F_R=0.5$), or above optimal sustainable levels ($F_R=1.0$) (Lonergan 2011). This PBR approach has the benefit of being relatively straightforward to apply to SRKW (e.g., Barre 2012),

$$PBR = 87 \left(\frac{0.04}{2} \right) 0.1 = 0.17 \text{ SRKW/Year}$$

Thus, PBR for SRKW would be a relatively small fraction of a whale per year. Despite its simplicity, the Panel doubts that PBR would be a practical performance measure for assessing impacts of Chinook salmon fisheries on SRKW recovery. First and foremost, PBR cannot be readily monitored or measured from actual data, which precludes using it in objectives or performance criteria as defined above. In contrast to fishery bycatch applications, where PBR is sometimes used to determine allowable impacts on marine mammals, one cannot observe killer whales being “removed” from the population. On the contrary, killer whales that disappear are rarely recovered and therefore the cause of death cannot be determined (NMFS 2011b). Since 2005, only one reported killer whale stranding was identified as a Southern Resident Killer Whale (cause of death was apparently a vessel strike) and none of the reported deaths were attributed to starvation (NMFS 2011b), which would be the assumed mechanism by which removals would be caused by Chinook salmon fisheries, unless there is an interaction between nutritional state and probability of ship strike or other source of mortality.

Determining whether Chinook salmon fisheries were responsible for indirectly removing 0.17 whales per year (or some fraction thereof) would require a highly precise model to allocate impacts of a suite of factors affecting SRKW abundance at any particular time. And it is increasingly clear that models taking multiple impacts on SRKW abundance and dynamics into account are not available at the present time.

Viable risk assessment procedure (VRAP): According to presentations in Workshop 2 (Barre 2012), VRAP defines the highest allowable exploitation that causes low risk to survival and high probability of long-term population recovery. The considerations described above for PBR similarly apply to VRAP. In particular, VRAP appears to be a simulation-based procedure for defining the risk adjustment factor F_R based on specific biological and policy-related reference points.

Biological criteria: Characteristics of SRKW populations, such as abundance, age-structure, sex ratios, social structure, and genetic diversity feature prominently in assessments of SRKW status, and likely continue to in the future, for both US and Canadian recovery strategies. Because biological characteristics are reasonably measureable, one way to improve the use of these criteria is to perform meta-analyses across a wide range of populations. At the present time, the only reference population for SRKW is the NRKW population, which may or may not be appropriate. As wide a range as possible in killer whale populations may provide a better empirical distribution against which to judge the future status of SRKW.

5.4 Recommended Information and Analyses

Key Question 4. Based on your expert opinion, are there additional analyses that could be conducted on the SRKW population or other resident killer whale populations to better understand the relationship between salmon abundance and killer whale population viability?

The Panel recognizes the considerable progress that has been made in understanding how salmon abundance may affect killer whale population dynamics. The analyses performed to date on the relationship between salmon abundance and killer whale fecundity and survival have likely extracted as much information as can be gained from the historical data. The results certainly lend credibility to the hypothesis that SRKW growth rates and abundance are related to salmon abundance, but they also raised many questions about specific mechanisms, the chance of spurious correlations, alternative hypotheses, data gaps, and expected changes in Chinook salmon availability. In the absence of controlled experiments, we will continue to rely on observational data, and therefore will remain unable to clearly distinguish among these alternatives in the future.

“If the effects of prey reduction on killer whale population dynamics cannot be adequately quantified, are there alternative frameworks for evaluating the risks of a particular level of prey reduction?” (Barre 2012)

Decision-analytic approaches and quantitative risk assessments are specifically designed to deal with irreducible uncertainties (Morgan and Henrion 1990). In general, much of the modeling work that has been done represents a form of quantitative risk assessment albeit with a specific focus on impacts caused by fisheries. However, clear indications that predation regimes faced by Chinook salmon are also changing raises considerable doubt that fisheries alone are having major impacts on SRKW dynamics. Therefore, as the Panel has attempted to communicate above, the Panel feels that an explicit set of “realistic” alternative hypotheses is missing from these analyses.

“Based on data and uncertainties, what criteria would be robust for assessing impacts of fisheries?” (Barre 2012)

There have not been many robustness tests of any performance measures for assessing impacts of fisheries of SRKW recovery. Robustness is about drawing the correct inferences and conclusions despite an incorrect perception of the underlying mechanisms. The Panel, as well as participants in the workshop process, has identified some alternative mechanisms and scenarios that should be investigated in greater depth, and perhaps one objective of those analyses should be to explicitly

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evaluate robustness of a suite of performance metrics at distinguishing among these hypotheses. In its draft report, the Panel suggested that simulation approaches be used to evaluate our ability to detect impacts of fisheries on SRKW under alternative scenarios. Although those specific suggestions did not survive interim reviews, the Panel continues to advocate for assessing robustness of performance measures via creative application of that approach.

Given the location and concentration of critical habitat, the SRKW population may be more exposed to industrial hazards than any other killer whale population in the world. Research characterizing potential catastrophic risks faced by SRKW associated with industrial accidents should continue to be a high priority.

If extinction risk criteria are central to recovery planning, then research on a wider range of factors than fisheries must be done, especially considering that significant expansion of oil tanker traffic in northern British Columbia would represent a much greater risk of catastrophic loss of SRKW (and NRKW) than fisheries. This suggestion is not meant to divert attention away from fisheries, but rather to recognize that modeled fishery impacts on SRKW extinction risk are probably not robust to other PVA assumptions.

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APPENDIX A: ORIGINAL QUESTIONS FROM THE NOAA AND DFO STEERING COMMITTEE

Original questions from the NOAA and DFO Steering Committee, as presented in the Reading List document:

1. What Do We Know about Their Feeding Habits?

Review the Available Information on Distribution, Diet, Food Energy Value of Prey, Daily Prey Energy Requirements of Southern Resident Killer Whales

- 1) Are the methods used to estimate the SRKW diet (including species, Chinook salmon stocks, and Chinook salmon age/size) scientifically reasonable given the available information? Do you have any suggestions to improve the methods?
- 2) Are the methods employed to estimate the daily prey energy requirements of the SRKW scientifically reasonable given the available information? Do you have any suggestions to improve the methods?
- 3) Based on your expert opinion, what level of confidence would you assign to the conclusion that, during the May-Sept time period in the Salish Sea, the SRKW have a diet consisting largely of Chinook salmon?
- 4) Based on your expert opinion, what level of confidence would you assign to the estimate of the distribution of age 3, 4 and 5 Chinook salmon in the SRKW diet (May-Sept, Salish Sea)?
- 5) Based on your expert opinion, what level of confidence would you assign to the conclusion that the SRKW's coastal diet largely consists of salmon? Of Chinook salmon?
- 6) Do you have specific suggestions to address key assumptions and uncertainties?

2. What Do We Know About Their Status?

Review the Available Information on Census and Population Structure, the Species Status and Recovery Criteria, Historical Abundance and Carrying Capacity of Southern Residents as well as Information about Northern Residents

- 1) What ecosystem considerations and/or trends might be relevant, including environmental carrying capacity questions?
- 2) Based on your expert opinion, what can we learn from evaluating the similarities and differences between Northern and Southern Resident?

3. What Do We Know About the Relationship Between Chinook salmon Abundance and Killer Whale Population Dynamics?

Review the Available Information on Demographic Modeling, the Role of Nutrition in Individual Growth and Condition, and Available and Emerging Methods to Investigate Body Condition

- 1) Are the methods employed to evaluate the relationship between salmon abundance and SRKW (and/or NRKW) fecundity, survival and population growth scientifically reasonable? Do you have any specific suggestions to improve the methods?

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- 2) Based on your expert opinion, are there additional analyses that could be conducted on the SRKW population or other resident killer whale populations to better understand the relationship between salmon abundance and killer whale survival, fecundity, and population growth?
- 3) Are the methods employed to evaluate the potential for nutritional stress in the SRKW population scientifically reasonable?
- 4) Based on your expert opinion, what level of confidence would you assign to the conclusion that the SRKW exhibit signs of nutritional stress? Of cumulative effects that include lower than optimal nutrition?
- 5) Are the methods employed to evaluate the viability of the SRKW under alternative assumptions about future salmon abundance scientifically reasonable? Do you have any specific suggestions to improve the methods?
- 6) Based on your expert opinion, are there additional analyses that could be conducted on the SRKW population or other resident killer whale populations to better understand the relationship between salmon abundance and killer whale population viability?

4. Identify Fisheries That May Affect Prey Availability

Review the Available Information on Fisheries That May Affect Prey Availability

- 1) Do any parts of these data need further clarification?

5. Chinook salmon Needs of Southern Resident Killer Whales

Review the NMFS and DFO's Analyses of the Population's Chinook salmon Needs. Based on this Information

- 1) Based on your expert opinion, what level of confidence would you assign to the conclusion that the SRKW prey energy requirements are within the range of Chinook salmon kilocalories or numbers of Chinook salmon estimated by NMFS and DFO?
- 2) Do you have specific suggestions to address key assumptions and uncertainties in the analysis?

6. Chinook salmon Abundance and Food Energy Available to Killer Whales

Review the Analysis Conducted to Date

- 1) Are the methods employed to predict salmon abundance by stock in specific times/places scientifically valid?
- 2) Are there improvements to the methods you would suggest?

7. Reduction in Chinook salmon Abundance and Food Energy from Fisheries

Review the Analytical Approach from the Opinion and NMFS Report on Fishery Profiles

- 1) Are the methods employed to predict the reduction in salmon abundance by stock in specific times/places scientifically valid?
- 2) Are there improvements to the methods you would suggest?

8. Ratio of Chinook salmon Food Energy Available Compared to Chinook salmon Food Energy Needed by Southern Residents with (and without) Fishing

Review the Analysis Conducted to Date

- 1) Are the methods employed to estimate the prey ratios under alternative fishing scenarios scientifically reasonable?
- 2) Do you have specific suggestions to address key assumptions and uncertainties?
- 3) How sensitive is the ratio analysis to its component parts? (e.g., selectivity function, whale population size and structure, percent of Chinook salmon in diet, food energy value of prey, etc.)
- 4) In your expert opinion, do forage ratios provide meaningful information about potential prey limitation in the SRKW?
- 5) How can we improve comparisons to ratios for other marine predators and systems?
- 6) What more can we learn from the ratios? For example, is it possible to estimate what the ratio should be in a given time and area to support survival and recovery of the whales?

9. Change in Population Growth Rates Annually, Abundance Over Time and Species Survival and Recovery

Review the Analysis Conducted to Date

- 1) Based on your expert opinion, what level of confidence would you assign to the conclusion that predicted changes in Chinook salmon abundance caused by fisheries affect the population growth rate of the SRKW?
- 2) Based on your expert opinion, what level of confidence would you assign to the conclusion that predicted changes in Chinook salmon abundance caused by fisheries increases the risk of extinction of the SRKW population?

APPENDIX B: COMPETING RISKS OF DEATH (CRD) MODELING

A competing risks of death (CRD) modeling framework for evaluating the impacts of alternative fishing regimes on prey availability and survival.

Throughout the workshop process, the Panel expressed concern about the assumptions underlying analyses of fishery impacts on Chinook salmon availability to killer whales. In particular, the Panel's view is that the original chain of logic linking fisheries to southern resident killer whales (**Figure 1A**) takes too narrow a view of the context in which these interactions take place. The Panel's original concerns arose following Workshop 1, where we questioned assumptions about constant Chinook salmon natural mortality rate and how eliminating Chinook salmon fisheries would cause direct increases in prey available to SRKW. Specific elements of these critiques are as follows:

- 1) **Chinook salmon natural mortality rates seem low** – Instantaneous natural mortality rates of approximately 0.2 year⁻¹ (~80% survival) and 0.1 year⁻¹ (~90% survival) for age-4 and age-5 Chinook salmon, respectively, seemed low given the overall magnitude of SRKW consumption of these age-classes (Noren 2011a, 2012) compared to total Chinook salmon abundance in the ocean (Kope 2012).
- 2) **Chinook salmon natural mortality should vary over time** - Temporal variation in Chinook salmon natural mortality would be a reasonable hypothesis given increases in marine mammal predators (especially NRKW and certain pinnipeds) over the past several decades (Ford 2012b, Pearson and Jeffries 2012).
- 3) **Chinook salmon natural mortality should be density-dependent** - Long-lived, highly mobile, and efficient specialist predators like SRKW and NRKW may be able to consume relatively stable quantities of Chinook salmon, which implies that the Chinook salmon natural mortality associated with killer whale predation should vary inversely with Chinook salmon abundance (i.e., at low Chinook salmon abundance, predation mortality should be higher than at high Chinook salmon abundance).
- 4) **Eliminating fisheries should cause an increase in Chinook salmon available to SRKW less than fishery impact** - SRKW are one of many competing consumers of adult Chinook salmon. The impacts of alternative fishing regimes on Chinook salmon available to SRKW does not account for consumption by these other consumers.

The above list contemplates a range of factors and processes that could be involved in Chinook salmon mortality processes. In this Appendix, we provide a brief description and numerical example of a competing risks of death (CRD; Heisey and Patterson 2006) modeling framework, which can help to frame evaluations of fishery-killer whale interactions in an ecosystem context. The CRD approach acknowledges that when multiple consumers act simultaneously as agents of [Chinook salmon] mortality (**Figure 1B**), one may not be able to predict the impact of adding or removing a source of mortality to overall survival rate without knowing how mortality caused by the remaining agents changes in response to this addition or removal (Heisey and Patterson 2006).

The CRD model we present below is not intended to replace existing multi-species analyses (e.g., Preikshot and Perry 2012) or Chinook salmon abundance reconstruction methods. Rather, it is meant to focus discussion on two types of confounding of fishery and predation effects that arise from the assumptions in (1)-(4) above. First, when there are multiple forces of mortality operating additively and independently on a common prey resource, and the fishing component ($F_{\text{fishing}} \sim 0.20$ year⁻¹) is relatively modest compared to other forces, then removing fishing as a cause of death will change prey survival rate less than F_{fishing} . Second, if the consumption of prey by natural predators is relatively constant (e.g., follows a Type II functional response), then the natural mortality rate of prey must vary, possibly dramatically, with prey abundance, being much higher when abundance is low.

Examining such interdependencies among multiple forces of mortality can be done using a CRD model that includes SRKW, NRKW, and fisheries as basic elements (although the more complex model in **Figure 1B** could be constructed from available information). The CRD approach takes various forms depending on the field in which it is applied. In fisheries, it takes the form of the so-called catch equation (Quinn and Deriso 1999), i.e.,

$$(1) \quad C_j(t) = N(t) \frac{F_j(t)}{Z(t)} (1 - e^{-Z(t)})$$

where j indexes prey consumer (e.g., 1=fishery, 2=SRKW, 3=NRKW), $C_j(t)$ is the total number of Chinook salmon harvested or consumed, $N(t)$ is the abundance of fully-selected Chinook salmon available to consumers at the beginning of period t , $F_j(t)$ is the force of mortality imposed by consumer j , M is a density-independent natural mortality rate from sources other than fisheries and killer whales, and $Z(t)$ is the total instantaneous mortality rate, i.e.,

$$(2) \quad Z(t) = M + \sum_{j=1}^J F_j(t)$$

The total annual survival rate is

$$(3) \quad S(t) = e^{-Z(t)}$$

Assumptions for the Numerical Example

Equation (1) can be solved for the unknown consumption C_j by each competitor if the individual forces of mortality F_j are known or predictable from either the product of catchability (q_j) and search time (E_j) (i.e., $F_j = q_j E_j$) or from historical estimates of exploitation rates derived from stock reconstruction methods. If, on the other hand, the F_j are unknown, then Equation (1) can be solved numerically for the F_j values given observed values for consumption or catch (C_j).

Below we provide a numerical example to demonstrate some basic inferences and insights that might be gained through application of the CRD, or similar, approach to the complex multi-predator/consumer context that provides the setting for these workshops. The example requires a

substantial number of simplifications and assumptions to allow a preliminary assessment of the implications of the CRD approach, and we recognize that some of these simplifications or assumptions may be more or less realistic. The most important simplifications/assumptions are as follows:

1. Fishery exploitation rates, F , for the historical period (1979-2005) were obtained from ocean catches, reconstructions of historical Chinook salmon ocean abundance, and estimated escapements (Kope 2012). It is important to note here that the ocean fishery exploitation rate estimates we used are dependent on assumptions about natural mortality rates at all life history stages via their use in reconstructing ocean abundances.

2. Chinook salmon consumption per killer whale (C) matches requirements as inferred from body growth models (Williams et al. 2011, Noren 2012). These consumption rates range from $C = 2435$ fish/year/whale for a low consumption scenario to $C = 3997$ fish/year/whale for a high consumption scenario. It is important to highlight here our key assumption that consumption of Chinook salmon per killer whale is fixed regardless of Chinook salmon abundance or the population age-/stage-structure of SRKW and NRKW. Although this is probably not a valid assumption in general, we assume it is a reasonable approximation for a preliminary assessment of the range of Chinook salmon mortality rates generated by killer whales. Fixing consumption this way will tend to over-estimate mortality rates at very low Chinook salmon abundance because there is no reduction in total Chinook salmon consumed by killer whales as perhaps might occur if total feeding time is limiting.

3. Chinook salmon natural mortality rates are assumed to be $M = 0.1/\text{yr}$ or $M = 0.2/\text{yr}$ from sources other than fisheries or whales (e.g., sea lions, seals). These represent natural mortality rates for age-4 and age-5 Chinook salmon as employed in existing modeling approaches (e.g., CTC, FRAM) and probably result in conservative assessments of mortality in the sense that predation mortality on age-4 and age-5 Chinook salmon by pinnipeds is assumed small compared to predation mortality caused by killer whales.

Results

Based on the low consumption scenario ($C = 2345$; $M = 0.1$), numerical results from the CRD model suggest that annual survival of ages 4-5 Chinook salmon varied between approximately 55% and 80% over the period 1979-2005. Early peaks of Chinook salmon total mortality in 1979-80 were associated with high fishing mortality, while later peak mortality (1991 and 2004) occurred when low Chinook salmon abundance combined with higher NRKW and SRKW abundances to produce high natural mortality rates (**Figure 2**). Since the early 1990s, it appears that natural mortality may have been substantially higher than assumed in current stock assessments for Chinook salmon.

At the lowest levels of Chinook salmon ocean abundances than have been experienced over the 1979-2005 period (less than 2.5-3.0 million), the CRD model suggests that SRKW and NRKW exert much higher predation mortality, which could lead to annual Chinook salmon survival rates below 40% under low consumption (**Figure 3** top row) and below 30% under high consumption scenarios (**Figure 3** bottom row), even at low fishing mortality.

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When Chinook salmon ocean abundance is greater than about 3.5 million, it appears that assumptions about natural survival rates of 80-90% are not unreasonable because mortality rates caused by killer whales would then be relatively low. Mortality due to killer whale predation is much less sensitive to changes in Chinook salmon abundance when that abundance is high.

Discussion

The CRD model examples are meant to sketch the types of analyses that could be done, for example as checks on the consistency of current assumptions and hypotheses about interactions among marine mammals, fisheries, and Chinook salmon mortality patterns. For the numerical examples above, we made what seemed like sensible assumptions for abundances and consumption rates given presentations at workshops and the available literature (much of which was written by workshop participants!). The results suggest nonlinear interdependencies in how Chinook salmon mortality is partitioned among fisheries, killer whales, and possibly other marine mammals. The CRD approach also suggests that natural mortality rates of Chinook salmon may have increased since the 1970s-1980s due to increasing abundance of northern resident killer whales especially. **Thus, one hypothesis arising from these calculations is that the NRKW population may exert as much, or more, influence over SRKW growth rate as fisheries.** Such relationships could be analyzed in the existing logistic regression framework.

The conceptual model in **Figure 1B** suggests a **second hypothesis that reducing ocean and pre-terminal fisheries may actually result in more transient killer whales (TKW)** via response of intermediate pinniped (PINN) predators to increases in available Chinook salmon.

Fixing the total consumption of Chinook salmon by SRKW and NRKW implies the strong assumption that killer whales impose depensatory mortality on Chinook salmon, as is demonstrated in **Figure 3**. We did not actually model Type II functional response behavior of whales, because that would require more complex analyses that are beyond the scope of our review, although the approach has been applied to other fishery-marine mammal conflicts (Trzcinski et al. 2006). Considering the functional response would likely be important if seasonality were taken into account. In winter, when Chinook salmon are more dispersed compared to peak density periods in summer, SRKW may not be able to consistently obtain a full ration as assumed in the above calculations. Therefore, a more realistic model would be based on input search effort and the functional response rather than assuming constant consumption.

Finally, we wish to acknowledge that estimates of Chinook salmon ocean abundance are based on reconstructions provided by the CTC. The CTC calculations assume that mortality rates between the fish ages are much less than those implied by our CRD calculations. For example, in the run reconstructions, numbers of age-3 fish estimated present in the ocean include an adjustment for ocean natural survival rate. If the true ocean natural survival rates were much less, then the estimated abundances at younger ages would be much more than currently calculated by the CTC. Such effects on age-4 would reflect just one year of "scaling up" to correct for unknown losses due to ocean natural mortality, while effects on age-5 would be small, reflecting only the part of the year (Winter-Summer) leading up to fisheries. Thus, we caution that the CRD calculations probably exaggerate the actual mortality rates, though the relative magnitude of forces of mortality may be

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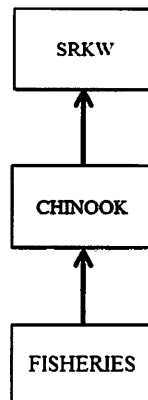
reasonable. On the other hand, we also ignore the dynamics of other Chinook salmon predators such as pinnipeds, which we assume contribute to the constant, relatively low natural mortality rate M , but which are probably more appropriately dealt with in the same fashion as for killer whale predation. It is likely that multispecies models like Ecosim could also represent the full suite of predation and fishing mortality impacts on Chinook salmon (Preikshot and Perry 2012).

A CRD or similar modeling approach provides a tractable means of assessing alternative "minimum-realistic" models (Punt and Leslie 1995, Yodzis 2001) for predicting how abundance of Chinook salmon and their predators might respond to alternative fishing regimes. The interactions among Chinook salmon, predators, and fisheries is certainly complex enough to warrant looking beyond single-species approaches.

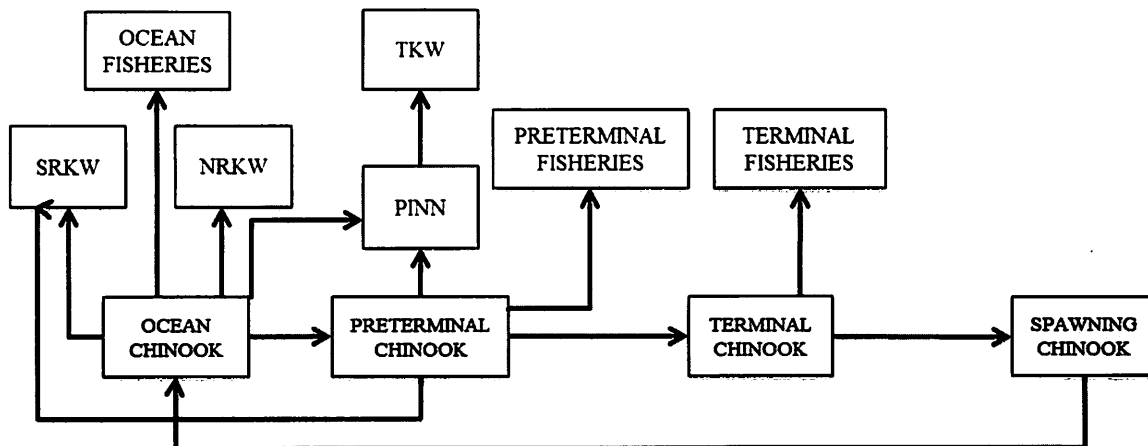
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Figure 1. Alternative influence diagrams for linking fisheries to Chinook salmon and Southern Resident Killer Whales. (A) Original logic diagram used to define and scope analyses of fishery impacts on SRKW population growth and viability. (B) Alternative influence diagram derived from a competing risks of death (CRD) conceptual model. The CRD is defined by Chinook salmon consumers in ocean (OCEAN), pre-terminal coastal (PRETERMINAL), terminal freshwater areas (TERMINAL), and spawning grounds (SPAWNING). Animal consumers are Southern (SRKW) and Northern (NRKW) Resident Killer Whales and pinnipeds (PINN). Consumers of pinnipeds are transient killer whales (TKW). Consumers of pinnipeds are transient killer whales (TKW).

A)

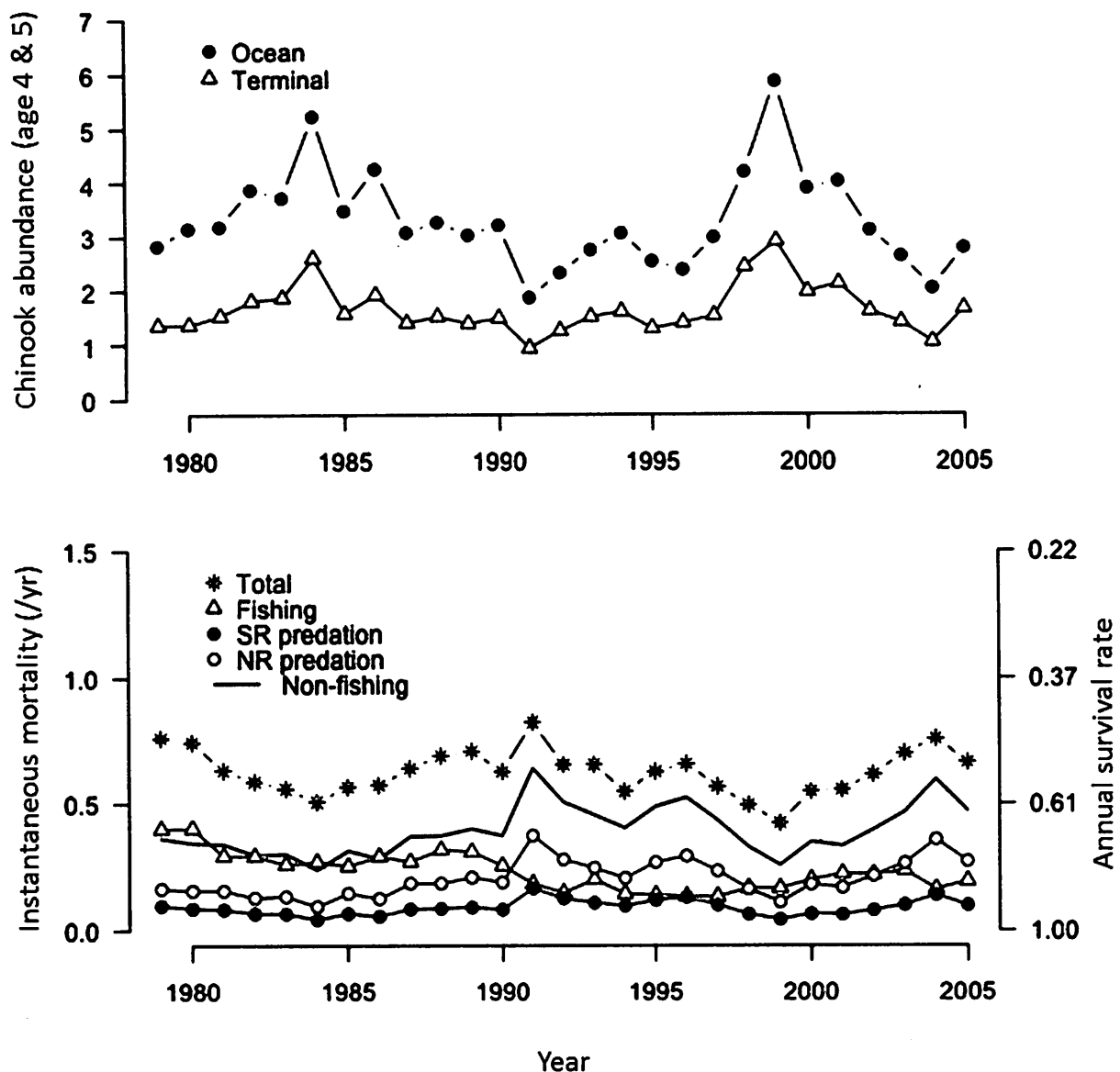


B)



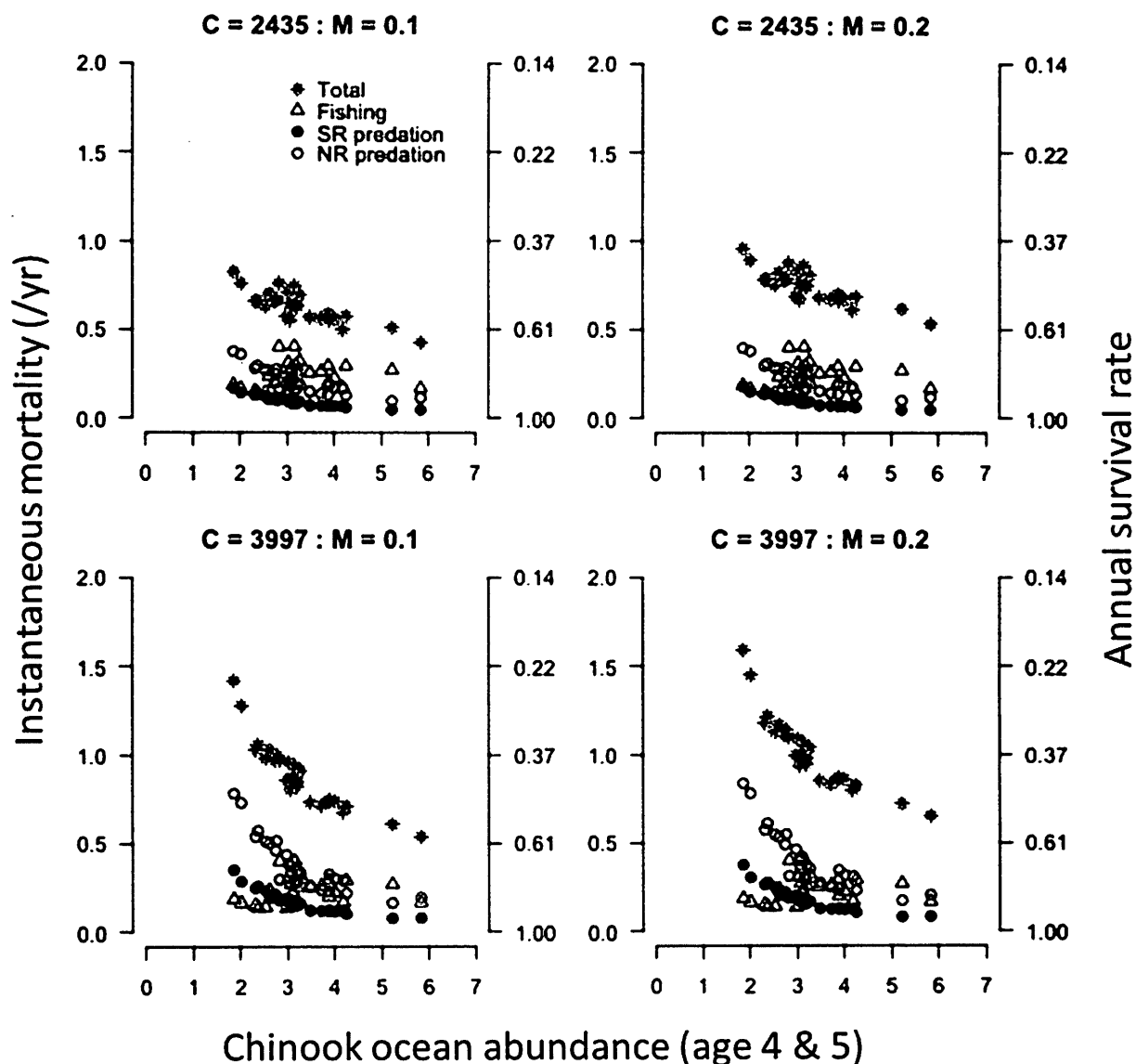
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Figure 2. Top: Ocean and Terminal Run Chinook salmon abundances obtained from "CTC model-based ERs.xlsx" spreadsheet (calculated as sum of age 4&5 combined Scohort and Terminal Runs). **Bottom:** Instantaneous mortality rates obtained by solving CRD model under assumptions that (i) SRKW and NRKW total annual consumption per whale is constant ($C=2435$ Chinook salmon in this example); (ii) historic fishing mortality rates are known; and (iii) Chinook salmon prey availability to killer whales is represented by reconstructed Ocean abundance. Total predation + natural mortality is shown as "Non-fishing" (solid red line). The axis on the right side shows the annual survival probabilities corresponding to the instantaneous mortality rates on the left.



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Figure 3. Relationships between Chinook salmon ocean abundance and the components of instantaneous mortality under four combinations of consumption rates (low and high range reported in Williams et al. 2011) and natural mortality rate from causes other than SRKW and NRKW predation.



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Competing tradeoffs between increasing marine mammal predation and fisheries harvest of Chinook salmon

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Many marine mammal predators, particularly pinnipeds, have increased in abundance in recent decades, generating new challenges for balancing human uses with recovery goals via ecosystem-based management. We used a spatio-temporal bioenergetics model of the Northeast Pacific Ocean to quantify how predation by three species of pinnipeds and killer whales (*Orcinus orca*) on Chinook salmon (*Oncorhynchus tshawytscha*) has changed since the 1970s along the west coast of North America, and compare these estimates to salmon fisheries. We find that from 1975 to 2015, biomass of Chinook salmon consumed by pinnipeds and killer whales increased from 6,100 to 15,200 metric tons (from 5 to 31.5 million individual salmon). Though there is variation across the regions in our model, overall, killer whales consume the largest biomass of Chinook salmon, but harbor seals (*Phoca vitulina*) consume the largest number of individuals. The decrease in adult Chinook salmon harvest from 1975–2015 was 16,400 to 9,600 metric tons. Thus, Chinook salmon removals (harvest + consumption) increased in the past 40 years despite catch reductions by fisheries, due to consumption by recovering pinnipeds and endangered killer whales. Long-term management strategies for Chinook salmon will need to consider potential conflicts between rebounding predators or endangered predators and prey.

Marine mammal population recoveries are a conservation success story in many parts of the world^{1,2}. Multiple legal protections put in place in the mid-20th century have resulted in recoveries of populations once threatened with extinction. For example, bans on whaling or prohibitions on imports of marine mammal products by the International Whaling Commission³, the Marine Mammal Protection Acts (US 1972, New Zealand 1978), Environmental Protection and Biodiversity Conservation Act (Australia 1999) and Species at Risk Act (Canada, 2002) have led to recoveries of some marine mammal populations. Further protections for some species were added under the US Endangered Species Act (ESA). In the Northeast Pacific Ocean, protection of marine

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mammals has led to recoveries of populations of humpback whales (*Megaptera novaeangliae*, 81 FR 62260; September 8 2016), and Steller sea lions (*Eumetopias jubatus*, 78 FR 66139; November 4 2013). Marine mammal populations never threatened with extinction also benefited from protection, with some populations recovering to high abundance levels (e.g. harbor seals *Phoca vitulina richardii*^{4,5}). Rates of recovery have been particularly strong for coastal species with relatively short generation times, such as pinnipeds: seals and sea lions¹.

The unintended consequences of marine mammal recoveries have created new tradeoffs for natural resource managers to confront⁶. Examples of potential impacts of higher trophic level consumers on other species in the food web include: reduced recovery of forage fish such as Pacific herring (*Clupea pallasii*)⁷, increased competition between marine mammal species that share the same prey, such as pinnipeds and killer whales (*Orcinus orca*) in the Northeast Pacific⁶, and lastly, increased direct competition between marine mammal populations and fisheries. The potential impacts of recovering top predators on fisheries has been controversial. For example, within the International Whaling Commission (IWC), some argue that rebounding baleen whale populations are responsible for reductions in commercially fished prey populations and certain whale species should therefore be culled, whereas others argue that natural fluctuations in targeted fish populations and fisheries management are responsible for declines in yield⁸.

The recovery of pinnipeds in the coastal ecosystems of North America demonstrates all three of these potential conflicts. For example, populations of harbor seals and grey seals (*Halichoerus grypus*) on the coasts of North America have increased dramatically since the 1970s. Recent work using ecosystem models highlights the potential impacts that such recoveries may have on commercially fished species^{9,10}. Like other generalist predators, quantifying the impact of these pinnipeds on prey species can be challenging because pinnipeds may consume fish at a variety of ages. For example, anadromous fish such as salmon may be consumed in estuaries as juveniles (as they leave streams to migrate to the ocean) or up to several years later as adults as they return to freshwater to spawn. A second challenge in quantifying the impact of these pinnipeds is that their diets vary in space and time, as predators alter their foraging to exploit local concentrations of prey.

In many other ecosystems around the world, there have been long-standing concerns about the potential impacts of marine predators on fisheries. On the west coast of the US and Canada, these concerns have been heightened because of external pressures on salmon populations (e.g. habitat loss). For example, over the last 20 years, multiple populations of Chinook salmon (*Oncorhynchus tshawytscha*), as well as Southern Resident and Northern Resident populations of salmon-eating killer whales, have been listed under the ESA or Canadian Species at Risk Act (SARA); the Southern Resident population is of particular concern due to both low population size and low population growth rate¹¹. Studies examining conflicts between marine mammals and fisheries were initiated in the NE Pacific in the late 1970s after marine mammals caused losses in salmon fisheries¹². Of the salmon species present on the west coast of North America, Chinook salmon are the largest and most valuable by weight. Chinook salmon migrate thousands of kilometers from their natal streams on the U.S. west coast to Alaska as juvenile fish, before returning 2–4 years later. The majority of salmon predation studies have focused on ‘hotspots’, including Puget Sound and the Columbia River, where there are apparent tradeoffs between local populations of pinnipeds and threatened or endangered salmon¹³. In most of these regions, genetic methods have recently been used to quantify the importance of salmon in diets of salmon-eating killer whales¹⁴ and pinnipeds¹⁵.

In the context of the global recovery of many marine mammals^{1,2}, here we quantify how marine mammal predation on Chinook salmon has changed since the 1970s along the west coast of North America (California to Alaska, including US and Canadian waters, Fig. 1), and compare this to salmon production and fishing mortality from commercial and recreational fisheries. Though Chinook salmon are consumed by a wide variety of predators, including birds, mammals, and other fish, the focus of our analysis is on the four marine mammal predators that have been previously documented to consume juvenile or adult Chinook salmon: harbor seals, fish-eating killer whales, California sea lions (*Zalophus californianus*), and Steller sea lions. Motivated in part by a recent peer-review of science to quantify the impact of salmon fisheries on Southern Resident killer whales¹¹, and concerns about the timing and prey base required to recover such populations^{16,17}, we place particular emphasis on interspecific competition between marine mammal species and specifically implications of changes for killer whales. We couple population data from the four marine mammal species and Chinook salmon to bioenergetics models and diet information. By examining spatial and temporal changes in consumption of Chinook salmon in the Northeast Pacific, we find evidence that salmon consumption by marine mammals has more than compensated for reductions in fisheries harvest from 1975–2015, which has implications for recovery of both endangered salmon and endangered killer whales.

Results

Total Chinook salmon smolt production on the west coast increased from the 1970s to the 1990s and has been relatively constant over the subsequent two decades (Fig. 2). Between 1975 and 2015 the estimated production of wild and hatchery Chinook salmon increased from 225 to 406 million juveniles (Fig. 2). In the 1970s and 1980s this was driven by an increase in production of hatchery fish. Since the mid 1980s, a decline in hatchery production has been offset by an increase in smolt production from some wild stocks, such as in the Columbia River.

Chinook salmon biomass consumed by the marine mammal predators was estimated to have increased steadily over the entire study period from 6,100 to 15,200 metric tons (Fig. 3a,b). The estimated increase in predation was directly related to increasing predator abundance used in our model. Killer whales increased from 292 to 644 individual resident killer whales, harbor seals increased from 210,000 to 355,000, California sea lions increased from 5,900 to 47,000, and Steller sea lions increased from 74,400 to 78,500. Killer whales consumed the most Chinook salmon biomass (from 5,400 metric tons in 1975 to 10,900 metric tons in 2015), followed by harbor seals (400 to 2,500 metric tons), Steller sea lions (300 to 1,200 metric tons), and California sea lions (50 to 600 metric tons). Numerically, the predator consumption increased from 5 to 31.5 million individual Chinook salmon of varying ages (Fig. 3c,d). This was largely driven by increased consumption by harbor seals (from 3.5 million to

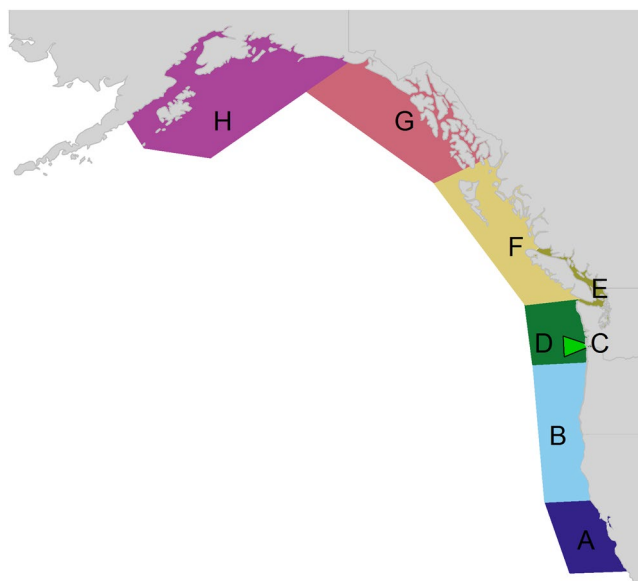


Figure 1. The eight areas in the study: Central California (A), northern California/Oregon (B), Columbia River (C), outer Washington coast (D), Salish Sea (E), West Coast of Vancouver Island and coastal British Columbia (F), Southeast Alaska (G), and the Gulf of Alaska (H). Map created using the maps package for R software⁶⁴.

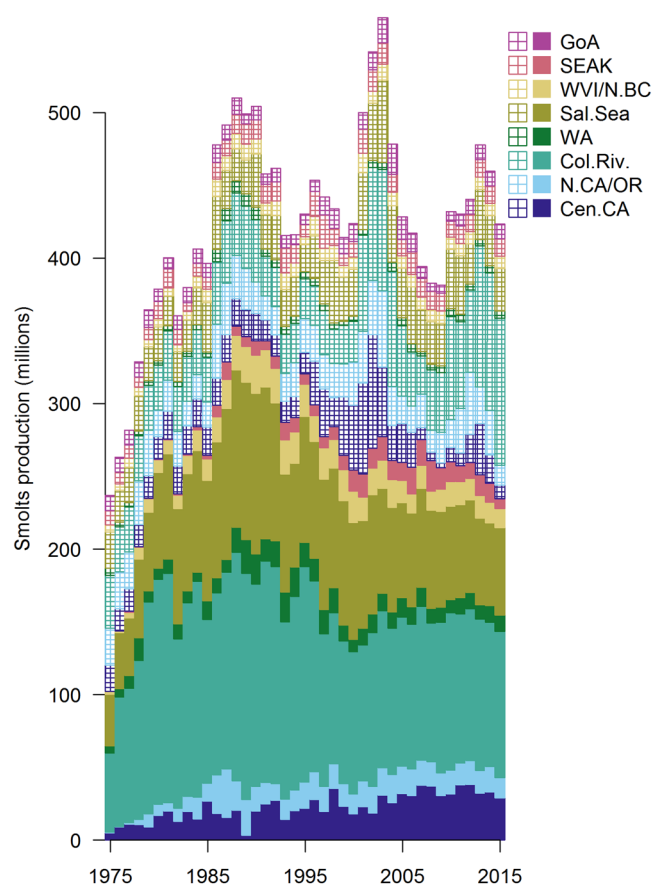


Figure 2. Natural (hatched) and hatchery (solid) Chinook salmon production by area between 1975 and 2015 for Central California (Cen.CA), Northern California/Oregon (N.CA/OR), Columbia River (Col. Riv.), outer Washington Coast (WA), Salish Sea (Sal. Sea), West Coast Vancouver Island and coastal British Columbia (WVI/N.BC), Southeast Alaska (SEAK), and Gulf of Alaska (GoA).

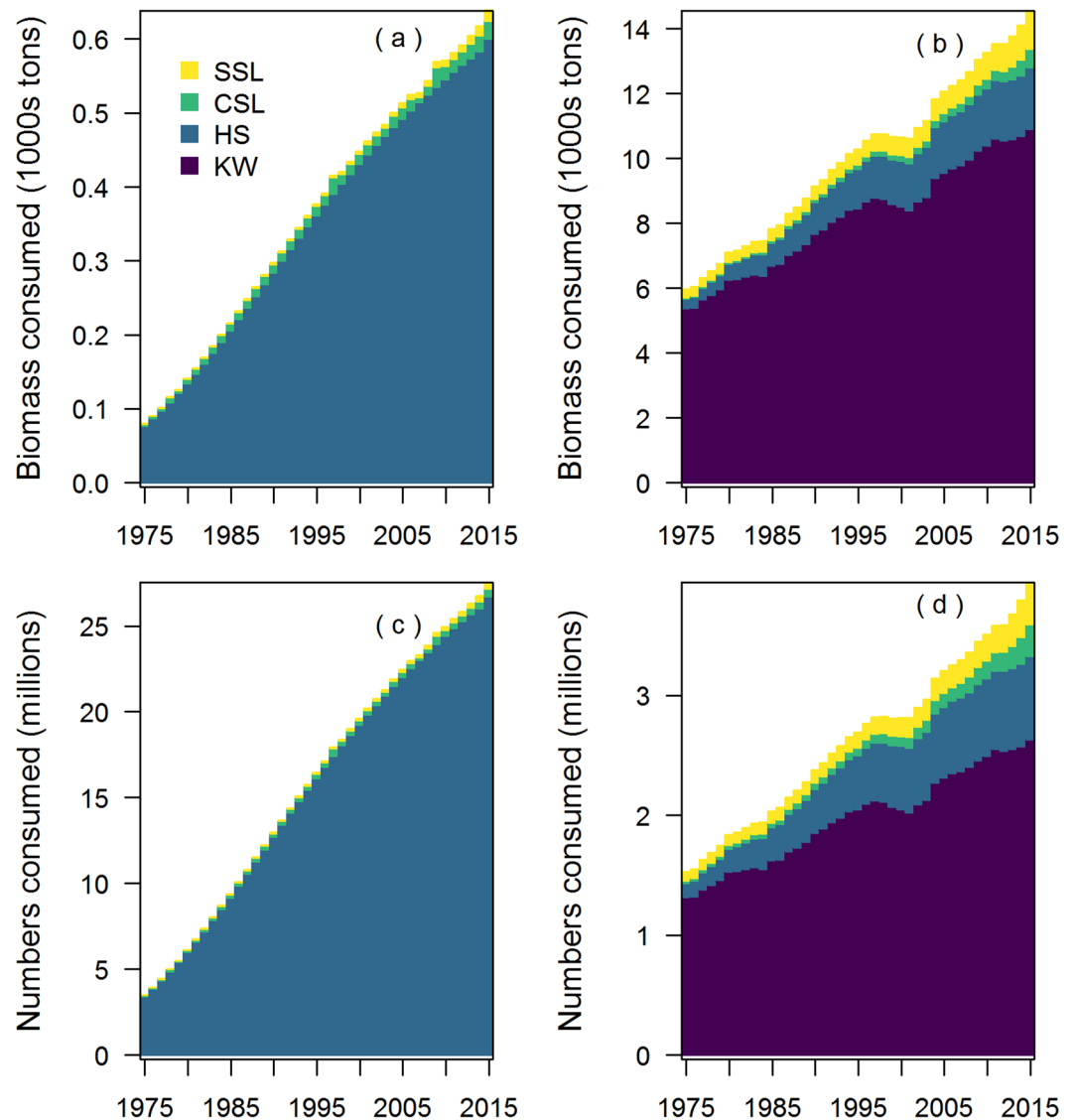


Figure 3. Consumption of Chinook salmon biomass ((a) juveniles, (b) adults ocean age one and greater) and total numbers ((c) juveniles, (d) adults ocean age one and greater) by killer whales (KW), harbor seals (HS), California sea lions (CSL), and Steller sea lions (SSL) from 1975 to 2015. Consumption is summed across all eight model areas shown in Fig. 1.

27.4 million individual Chinook salmon), followed by killer whales (1.3 to 2.6 million), California sea lions (0.1 to 0.7 million), and Steller sea lions (0.1 to 0.7 million).

Pinniped consumption of juvenile Chinook salmon was a substantial component of predation mortality coast-wide, but particularly in the Salish Sea. Of the estimated 27.4 million Chinook salmon consumed coastwide by harbor seals in 2015 (Fig. 3), 23.2 million were smolts consumed in the Salish Sea. The percentage of the total coastwide smolt production consumed by harbor seals increased from 1.5% (3.5 million consumed out of 236.8 million estimated total production) in 1975 to 6.5% (27.4 million consumed out of 423.4 million estimated total production) in 2015. Harbor seals in the Salish Sea (i.e. Puget Sound, Strait of Georgia, and Strait of San Juan de Fuca) accounted for 86.4% of the total coast wide smolt consumption in 2015, due to large increases in the harbor seal abundance in this region between 1975 and 2015 (8,600 to 77,800), as well as a large diet fraction of Chinook salmon smolts relative to other regions (see supplemental material).

While predation on Chinook salmon by marine mammal predators increased, annual harvest by commercial and recreational fisheries decreased from 3.6 million to 2.1 million individuals, equivalent to 16,400 to 9,600 metric tons (Fig. 4a). At the same time, predator consumption of Chinook salmon increased from 1.3 to 3.1 million adults (we exclude smolts and ocean age one jacks from the estimate because they are not retained in fisheries), or from 5,800 to 14,200 metric tons. The change in predation and harvest was not evenly distributed across Chinook salmon from different areas (Fig. 4). Generally, for Chinook salmon from natal stocks in the south (Central California, Northern California/Oregon, and Columbia River), predation impacts have increased strongly over time and exceeded harvest in recent years. These stocks' longer migrations northward expose them

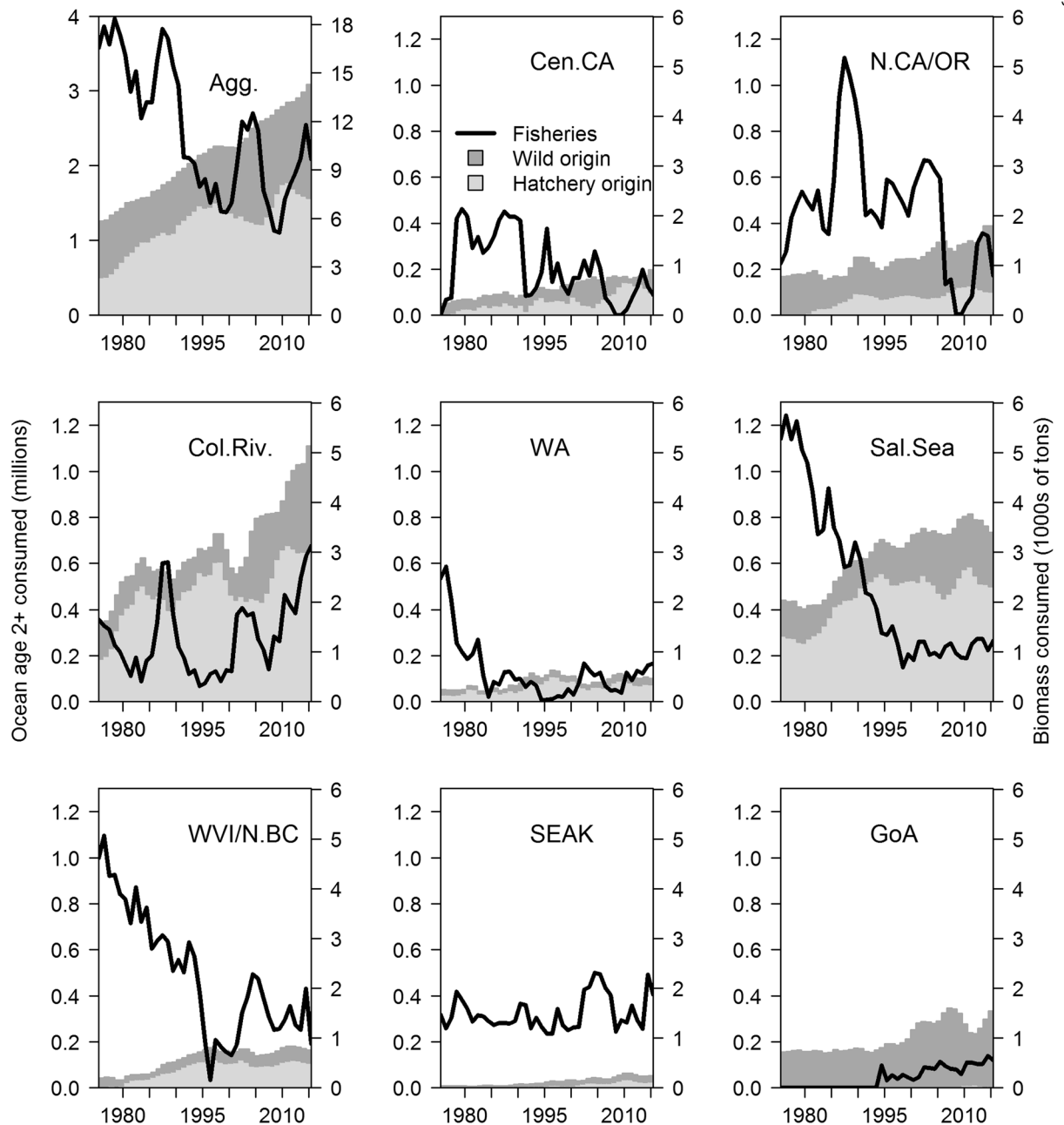


Figure 4. Total numbers (millions; primary axis) and biomass (thousands of metric tons; secondary axis) of adult Chinook salmon removed by fisheries (line) and the combined marine mammal predators (shaded areas) from 1975 to 2015. The top left panel sums over the whole model domain; each other panel represents hatchery and natural Chinook salmon stocks from a single area of origin. Note that estimates of predation in these panels include Chinook salmon consumed by marine mammals throughout the migratory range of that salmon stock (salmon originating in SEAK are consumed by marine mammals in Alaska, while salmon originating from Washington are potentially consumed by marine mammals in Washington, British Columbia, and Alaska).

to a gauntlet of predators throughout our modeled regions. Predation has also increased on Northern Chinook salmon stocks (Washington, W.Coast Vancouver Island and coastal British Columbia, and Southeast Alaska), but for these stocks predation is presently near or below the harvest. For Salish Sea Chinook salmon, strong increases in predation greatly exceed harvest; this is driven largely by local increases in pinniped abundance in the Salish Sea. Similarly, Chinook salmon from Gulf of Alaska stocks have experienced increasing predation (which exceeds harvest), due to local abundance of killer whales (including Gulf of Alaska and Southeast Alaska Resident killer whales).

Killer whales are the largest consumers of Chinook salmon biomass among the predators in our model, accounting for 10,900 of the total 15,200 metric tons biomass consumed in 2015 (Fig. 5b). Since 1975, the largest increase in consumption has been from the Northern Resident killer whales along the West Coast Vancouver

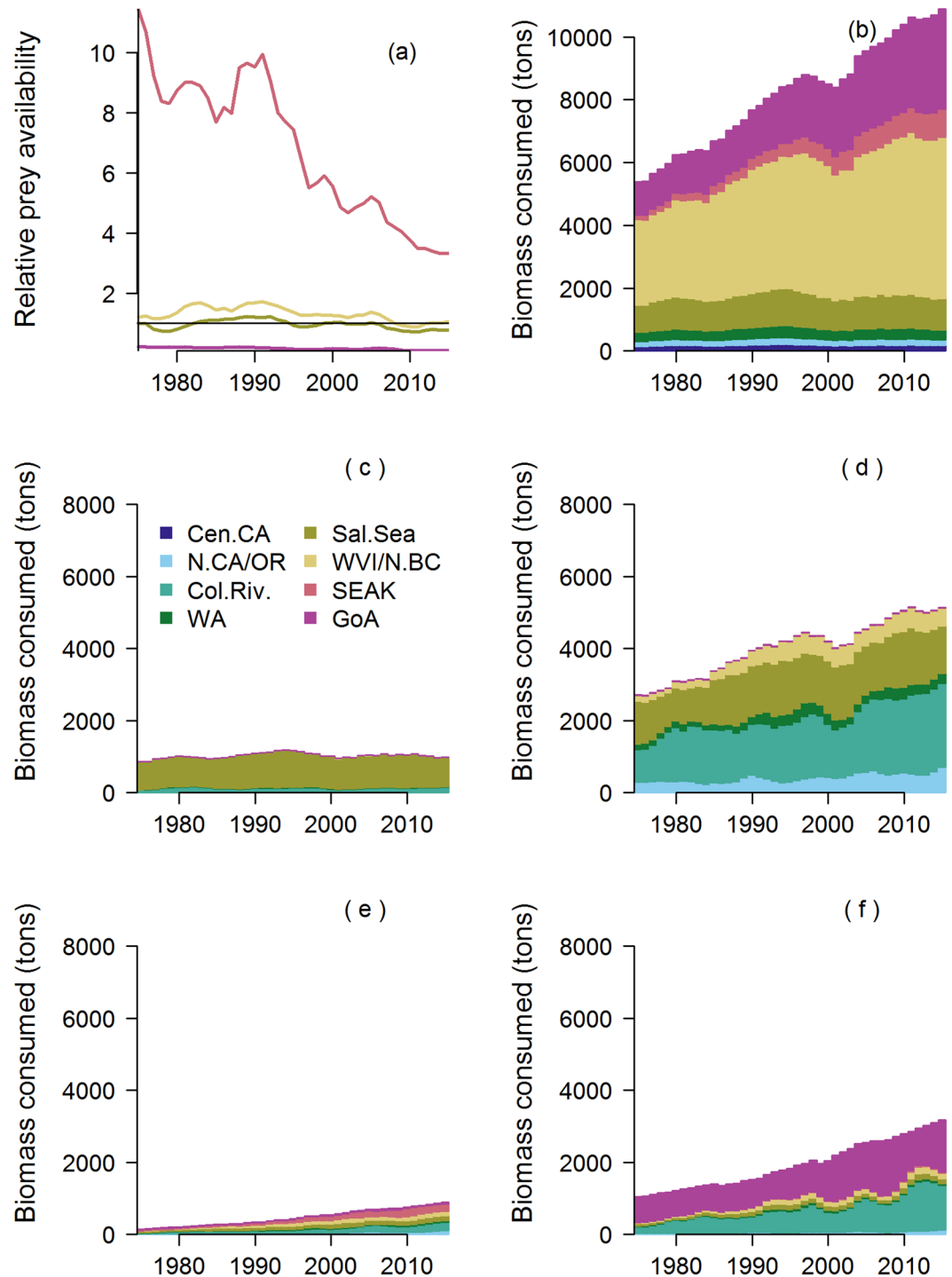


Figure 5. Estimates of the relative ratio of available adult Chinook salmon prey (equation (3)) to killer whale consumption of Chinook salmon in each ocean region ((a) equation (6)), estimated total Chinook salmon consumption by killer whales in each ocean region (b), and the estimated contribution of Chinook salmon originating from different ocean regions to composition of Chinook salmon consumed by killer whales in the Salish Sea (c), West Coast Vancouver Island and coastal British Columbia (d), Southeast Alaska (e), and Gulf of Alaska (f).

Island and coastal British Columbia (Fig. 5d), approximately 2,400 metric tons. The combined increase in consumption for the Southeast Alaska Residents and Western Alaska Residents from 1975 to 2015 was equal to about 2,900 metric tons. The Southern Resident population in the Salish Sea has remained relatively stable, and therefore the annual consumption within Salish Sea waters has been relatively constant at 900 to 1,200 metric tons, equivalent to about 190,000 to 260,000 adult Chinook salmon annually.

All regions exhibited declines in availability of Chinook salmon as prey for killer whales, even though killer whales in each region depend upon different Chinook salmon stocks. The ratio between Chinook salmon available as prey and the diet needs of the killer whales is estimated to have declined along the entire west coast during the last 40 years (Fig. 5a), although ratios for coastal British Columbia and Southeast Alaska were consistently higher than for the Salish Sea. We estimated that killer whales within each region depend upon Chinook salmon from distinct populations: the Southern Resident killer whale diets are dominated by Salish Sea Chinook salmon (Fig. 5c), Northern Resident killer whale diets are primarily Salish Sea and Columbia River Chinook salmon (Fig. 5d), Southeast Alaska Resident diets are more uniformly distributed across Chinook stocks from all regions (Fig. 5e), and Western Alaska Resident diets are likely to be dominated by Gulf of Alaska and Columbia River Chinook salmon stocks (Fig. 5f).

The Columbia River has previously been identified as an area with high marine mammal consumption of salmon¹⁸, and our results for this region illustrate the relative impacts of different predators and how this varies across salmon life stages. In 2015, harbor seals consumed just 14 metric tons of Chinook salmon versus the 219 and 227 metric tons consumed by California and Steller sea lions, respectively. Considering the consumption of just adult (ocean age two and older) Chinook salmon in 2015, we estimated that harbor seals consumed 1,000 adult Chinook salmon, California sea lions consumed 46,000, and Steller sea lions consumed 47,000. Harbor seals, however, likely prey substantially on out-migrating smolts, and we estimate they would have eaten 312,000 smolts in 2015.

Including uncertainty in four key parameters related to predator abundance, diets, and bioenergetics does not qualitatively change the trends and relative impacts of the predators described above. Given uncertainty in these parameters, the estimated total biomass of Chinook salmon consumed in 2015 was between 12,400 and 18,700 metric tons for 95% of the simulations. The total number consumed varied between 12.5 million and 59.8 million individuals; this has higher relative uncertainty than biomass because it additionally incorporates uncertainty in smolt size and smolt fraction parameters. In 2015, approximately half of the uncertainty in the estimated total biomass of Chinook salmon consumed by marine predators can be attributed to killer whales (8,900 to 13,600 metric tons, Fig. 6a), while almost all of the uncertainty in the total number of Chinook salmon consumed can be attributed to harbor seals (9.2 to 54.9 million individuals, Fig. 6b). Across areas there is a similar pattern of uncertainty related to these predators (Fig. 7): in 2015 coastal British Columbia had the largest killer whale population among areas (261) and it also had the largest uncertainty in biomass consumed (4,300 to 6,500 metric tons; Fig. 7f), while the Salish Sea had the largest harbor seal population (78,000) and largest uncertainty in the number of Chinook salmon consumed (8.1 to 46.9 million) (Fig. 7e).

Discussion

Competition between fisheries and predators, such as marine mammals, has been a concern around the world, particularly as recent increases in predator populations have coincided with declines in some of their fish prey populations. Most studies attempting to quantify fishery losses to predation or damage to fishing gear caused by marine mammals have been localized to hotspot areas of conflicts. Our spatio-temporal model of marine mammal – Chinook salmon interactions is novel in that we quantified consumption of a highly migratory fish species by marine mammals over a broad spatial range, and across the entire fish life cycle in marine and estuary waters. We estimate that marine mammal consumption of Chinook salmon has increased dramatically over the past 40 years, and may now exceed the combined harvest by commercial and recreational fisheries in Central California, Northern California/Oregon, the Columbia River, the Salish Sea, and the Gulf of Alaska (Fig. 4).

Our main finding, that marine mammal consumption of Chinook salmon has increased dramatically over the last 40 years and likely exceeds removals by fisheries, was robust to a range of uncertainties in input parameters. Link *et al.*¹⁹ identify the need and challenge of addressing uncertainty in ecological models; in the framework of those authors we primarily addressed parameter uncertainty stemming from observation error and natural variability in key aspects of Chinook salmon and marine mammal biology. Though we did not address structural uncertainty in the model formulation, for instance by applying a multi-model framework^{19–21}, this would be possible by comparing our bioenergetics approach to other methods such as individual-based models²² or time series modeling approaches²³. Best practices for applications of ecological models²⁴ suggest consideration of multiple models, addressing parameter uncertainty, and understanding that models such as ours are strategic tools to identify major tradeoffs and explore hypotheses.

Implications for salmon recovery. Increased consumption demand of growing marine mammal populations in the Northeast Pacific could be masking the success of coastwide salmon recovery efforts. For example, long term reductions in the salmon available for commercial and recreational fisheries may not reflect lower abundance of salmon, but rather a reallocation from human harvest to marine mammal consumption. Because many populations of Chinook salmon in the Northeast Pacific are of conservation concern, substantial resources have been invested to improve salmon passage through hydropower dams²⁵, restore salmon habitat²⁶, reduce fishing²⁷, and otherwise improve conditions in rivers and streams to improve productivity. Collectively, these recovery efforts may have increased Chinook salmon survival or recovery, but these increases in salmon populations may be offset by salmon consumption by more-rapidly increasing populations of marine mammals and other predators. Samhouri *et al.*¹⁷ point out the challenges of this type of “predator-first” recovery, versus synchronous recovery of both predator and prey.

Predation of Chinook salmon by marine mammals in well-studied ‘hotspots’ (e.g. Salish Sea, Columbia River) is well known, but our results suggest additional predation in the ocean may be greater than previously documented. For instance, our estimates of in-river consumption of adult (ocean age two and greater) Chinook salmon by sea lions in the Columbia River from January to August in 2015 is 65,000 (49,000–81,000), which is lower than the most recent direct, tagging-based estimate of 95,000 (61,000–127,000) spring/summer Chinook

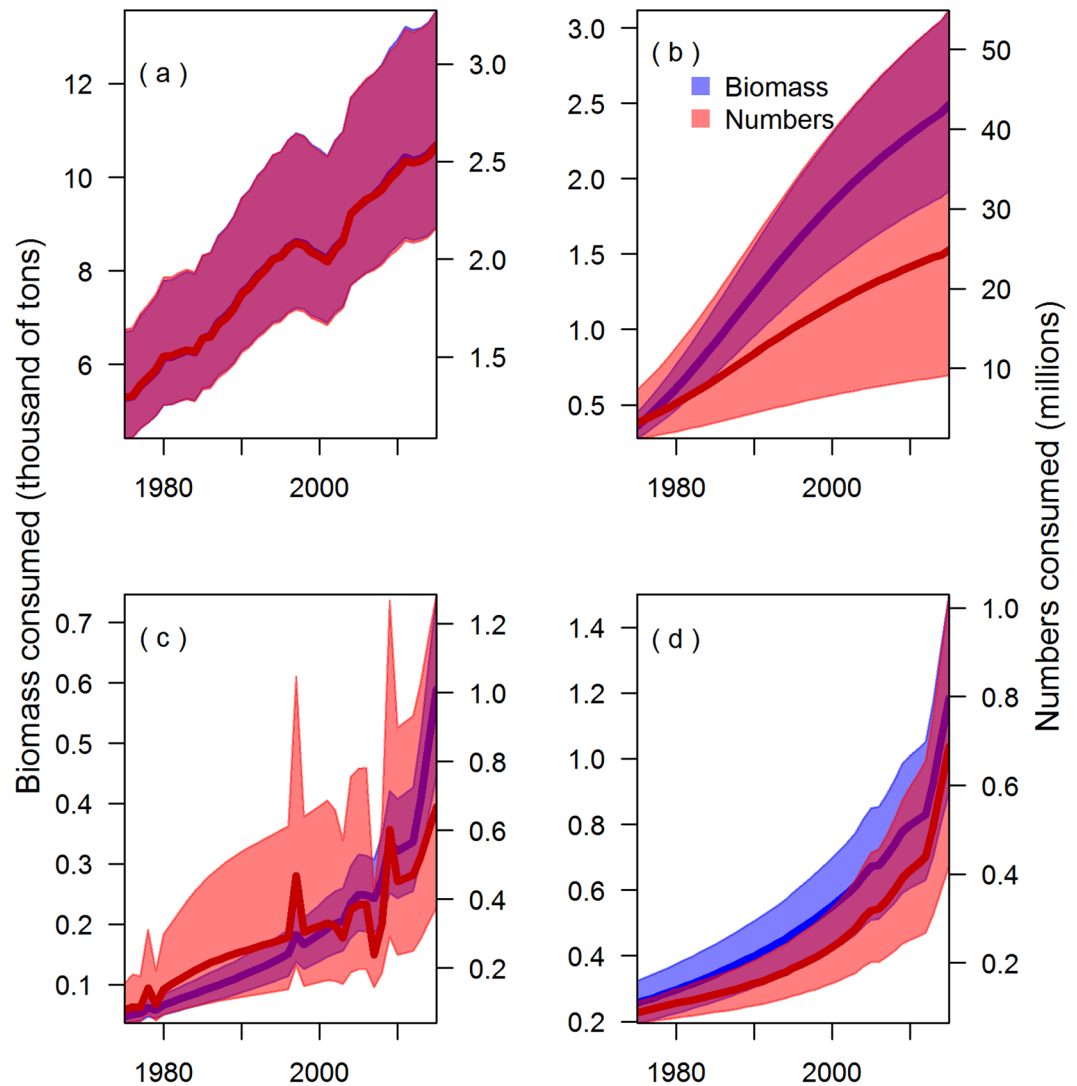


Figure 6. Estimates of consumption of Chinook salmon, with 95% confidence intervals, in terms of the annual biomass (primary axis; blue) and number (secondary axis; orange). Consumption by killer whales (a), harbor seals (b), California sea lions (c), and Steller sea lions (d). The red implies where the relative magnitude of uncertainty for the biomass and numbers overlap.

(Michelle Rub, pers. comm, August 7th, 2017). However, our model estimates sea lions consumed approximately 70,000 ocean age one Chinook salmon during the same period. Chinook salmon are also highly migratory, and our model allows salmon to be susceptible to predation throughout their range. Each salmon population has a unique distribution in the ocean²⁸, which affects the encounter rates by fisheries and predators; for example, southern Chinook salmon populations in our model have longer migrations and generally were susceptible to a larger number of marine mammal populations and associated predation. From the perspective of predator populations or fisheries, northern regions have a wider portfolio of Chinook salmon populations available to harvest²⁹.

Though not a direct focus of our analysis, approximately half of the Chinook salmon consumed by marine mammals or available to fisheries are of hatchery origin. Hatchery releases are conducted to increase fishing opportunities and assist salmon recovery efforts by helping supplement wild populations of conservation concern³⁰. An unintended effect of these programs is that they may contribute to unforeseen interactions between wild and hatchery origin fish. Though our model did not include different predation rates depending on salmon origin (hatchery, wild), it is possible that hatchery origin salmon provide a subsidy for marine mammals, leading to a numerical response in these predators and ultimately an increase in predation rates on wild fish. Alternatively, if marine mammals are generalist predators that lack a strong numerical response to increased salmon abundance, but nonetheless prefer Chinook salmon and seek them out relative to other prey, then hatchery Chinook salmon could lessen predation rates on wild fish. Exploring these dynamics would require modeling the functional response between Chinook salmon and marine mammal predators, and may be a fruitful avenue for future research.

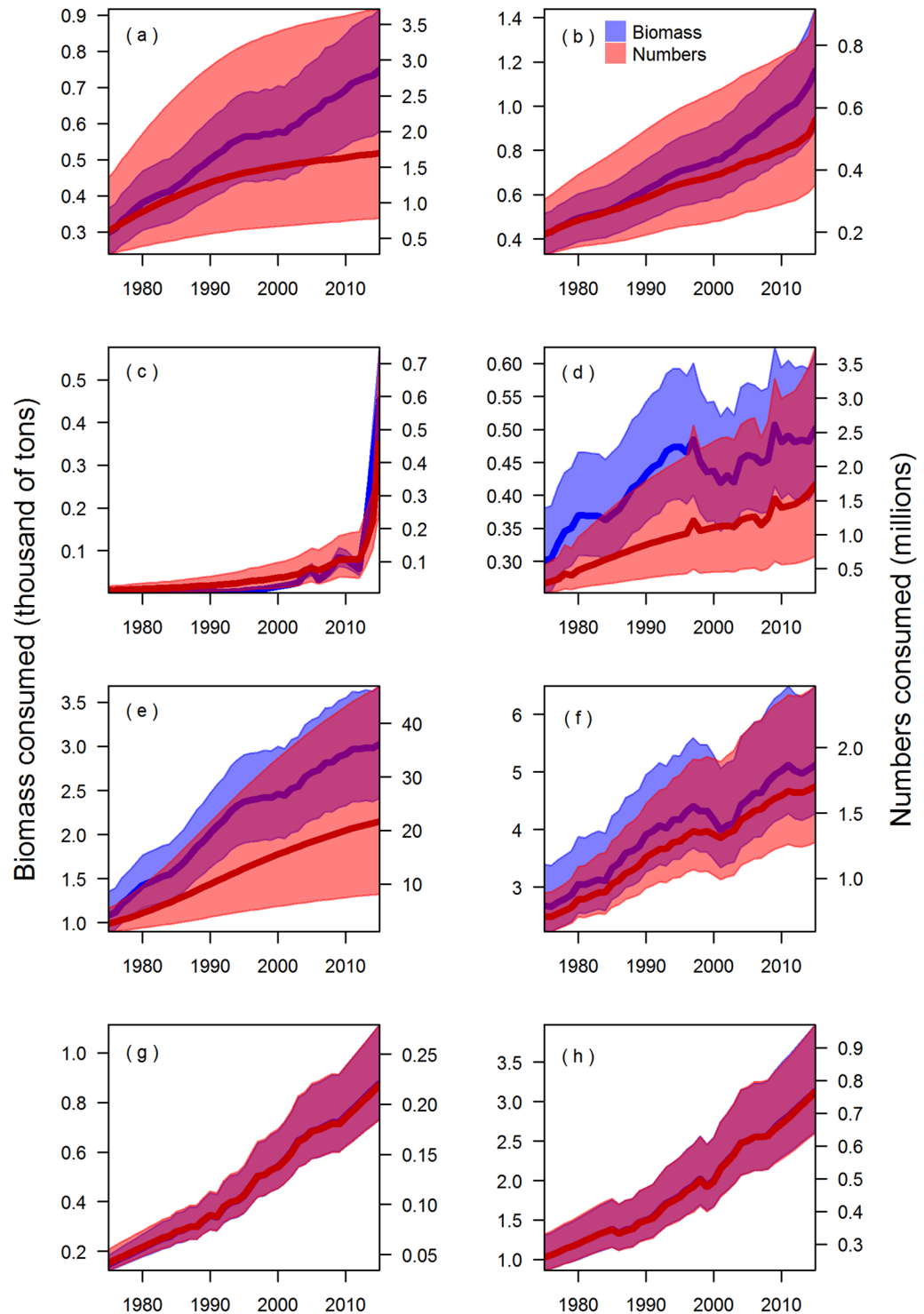


Figure 7. Estimates of consumption of Chinook salmon by the combined marine mammal predators, with uncertainty, in terms of the biomass (primary axis) and number (secondary axis) of Chinook salmon consumed per region: Central California (a), Northern California/coastal Oregon (b), Columbia River (c), Washington coast (d), Salish Sea (e), West Coast Vancouver Island and coastal British Columbia (f), Southeast Alaska (g), and Gulf of Alaska (h).

Implications for killer whale recovery. The abundance and diversity of Chinook salmon populations available as prey may have particular significance to predator populations that specialize on these populations as prey, such as fish-eating killer whales. Multiple populations of killer whales occur throughout the migratory range of Chinook salmon. Most of the salmon populations originating from natal streams on the west coast of the

US and Canada migrate northward to Alaska, so killer whale populations inhabiting Alaskan waters have a much broader range of salmon populations available as prey. In contrast, the most southern population of killer whales (Southern Resident killer whales), distributed in the Salish Sea and west coast of the US, is the most at-risk population with a long-term growth rate close to zero¹¹, and a much smaller diversity of salmon populations available as prey. This narrower selection of Chinook salmon stocks available to Southern Resident killer whales may be a competitive disadvantage compared to higher latitude killer whale populations. Increasing consumption of Chinook salmon by pinnipeds may also be limiting the growth of the Southern Resident killer whale population. Our results suggest that at least in recent years competition with other marine mammals is a more important factor limiting the growth of this endangered population than competition with human fisheries.

Future work. Though we conducted full sensitivity analyses on important model parameters, there are some potential sources of error that were not included. One obvious uncertainty is the ocean distribution of Chinook salmon. Available data on Chinook salmon distribution (following²⁸) may not fully describe the temporal and spatial overlap between predators and Chinook salmon (particularly juveniles), especially during the period of rapid growth during the first months in salt water³¹. While higher resolution of the temporal and spatial distribution of salmon populations would be useful, the geographic range and high rates of mortality make tracking fine scale movement and distributions difficult. Currently the best available information is based on coded wire tags recovered from commercial and recreational fisheries, not a systematic sample of the Chinook salmon distribution. Further, these distributions are assumed constant across years, which may be unrealistic, particularly if Chinook salmon have experienced distribution shifts in response to recent fluctuations in marine conditions³². A second potential source of error is in the proportion of Chinook salmon in predator diets. Data on diet fraction are informed by recent syntheses^{9,33} and updated field and laboratory methods^{14,15}, but nonetheless future work could consider more ecologically realistic (but complex) functional responses that include flexible diets of predators. For generalist predators such as pinnipeds, this would necessitate modeling multiple prey species. A third important assumption is that individual populations of Chinook salmon have not experienced trends in mean length, weight, or energetic content. Long term studies of Chinook salmon sizes in the ocean have shown significant reductions in growth rates (length-at-age³⁴ and weight-at-age^{35,36} of adult Chinook salmon with the exact mechanism for this decline not known. Because the relationship between fish length and weight (or energy) is non-linear, small decreases in adult length can lead to large differences in the number of salmon consumed – this is particularly true for killer whales^{37,38}.

Bioenergetics models such as ours are dependent on both historic and contemporary data collection efforts. This is particularly true for our spatially and temporally explicit model, because many parameters vary seasonally or over geographic regions. In using models such as ours to provide guidance to decision makers about tradeoffs, it is important for estimates to be both accurate and precise. Though it may be unrealistic to collect data on predators and prey at a fine scale, overall uncertainties would be reduced by balancing samples between historic predation hotspots and regions that have lower densities of predators but nonetheless substantial predation rates (e.g. coastal British Columbia, pinnipeds in the lower Columbia River). This will improve predictions about future impacts of predation on salmon and salmon fishing, and about tradeoffs and conflicting objectives of mandates such as the Marine Mammal Protection Act and the Endangered Species Act. Furthermore, our bioenergetics model does not “close the loop” on the full life-cycle of the Chinook salmon. Such an effort may provide estimates of the competitive interactions between the marine mammals and fishing sectors - instead of the relative ranking of their demands which we have provided. However, this future effort would require a more detailed reconciliation of the differences between the temporal and spatial availability of Chinook salmon to the marine mammals and fisheries, and more detailed estimates of the escapement and smolt production for the wild stocks to create a feedback between consumption and future production.

Methods

Model overview. We estimated the consumption of Chinook salmon by killer whales, harbor seals, and California and Steller sea lions to determine the location, source, and timing of predation mortality in the eastern Pacific, 1975–2015. Using bioenergetics models and information regarding marine mammal diets, we calculated this predation demand, and we then transformed the amount of energy each predator derived from Chinook salmon into estimates of biomass and numbers of Chinook consumed. Because marine mammal predators consume Chinook salmon of different sizes/ages, we used a Chinook salmon life cycle model to link the cohort abundance to predation demands in space and time. We provide a detailed description of the data in the appendix, and reserve the methods for describing how the data are incorporated into the bioenergetics model.

Predator dynamics, distribution, and energy demands. Estimates of marine mammal abundance were based on surveys by state and federal agencies (see supplemental material of model input). Years with missing survey data were interpolated by fitting logistic or exponential models to the survey data. Killer whales and sea lions are highly mobile, including migrations beyond their core ranges, and we therefore assembled information in the literature to determine temporal/spatial distribution of these species across areas and over seasons. Examples of detailed temporal/spatial patterns include that Southern Resident killer whales (SRKW) feed in the Salish Sea during the summer but leave during the winter months³⁹, Northern Resident killer whales occupy the waters of west Vancouver Island and British Columbia coast^{40,41}, and Southeast Alaska Residents and Gulf of Alaska Residents split their time in different areas of Alaska⁴². California and Steller sea lion populations in the Salish Sea and Columbia River areas exhibit a bi-modal distribution – feeding on spring and fall runs of returning adult salmon and returning to colonies along the outer coasts in summer and winter. Harbor seals in each region were assumed to be resident⁴³ with no exchange between populations in adjacent areas.

Because a predator's energy demand is determined by its mass⁴⁴, we combined weight-at-age models with information about the abundance, sex and age structure of the population to determine the total mass of the predator population in each area. For Southern Resident killer whales the age and sex distributions are known with perfect detection⁴⁵, but populations in Northern British Columbia and Southeastern and the Central Gulf of Alaska⁴² are estimated based on mark-recapture observation with imperfect detection. Sex and age distributions for harbor seals⁴⁶, California sea lions⁴⁷ and Steller sea lions⁴⁸ were estimated from survival tables; however, only California sea lions age six and older are assumed to consume Chinook salmon (pers. comm. J. Laake, NOAA AFSC). In some regions, such as the Salish Sea⁴⁹ or Columbia River, populations of sea lions are thought to be predominantly male, and thus females were excluded from these model regions.

Chasco *et al.*⁹ developed a modeling framework that calculated bioenergetics (energy) needs for the four marine mammals in Puget Sound. Here we apply an extended version of that model for the eight regions in the broader northeast Pacific. Daily energy ($ED_{p,h,j,y,t,i,a,s}$; Eq. 1; kcal/day) obtained through consumption of Chinook salmon for a predator population was estimated using Kleiber's model of basal metabolic rate⁴⁴. To transform BMR into field metabolic rate (FMR), which accounts for species and sex specific activity patterns, we multiplied the Kleiber model by a dimensionless scaling factor ($\alpha_{p,i,s}$) for killer whales⁵⁰, harbor seals⁵¹, California sea lions⁵² and Steller sea lions⁴⁸. Total needs were calculated by multiplying these factors by the product of the predator abundance ($N_{p,h,y}$), the proportion of a predator population that is age i ($PA_{p,h,y,i}$), sex ratio ($PF_{p,h,y,i}$), fraction of total energy derived from Chinook salmon ($FEC_{p,j,t}$), the selectivity of different age Chinook salmon ($SEL_{p,j,t,a}$), and the matrix describing the temporal and spatial distribution ($\Phi_{p,h,j,t,s}$),

$$ED_{p,h,j,y,t,i,a,s} = \Phi_{p,h,j,t,s} \times SEL_{p,j,t,a} \times FEC_{p,j,t} \times N_{p,h,y} \times PA_{p,h,y,i} \times PF_{p,h,y,i} \times \frac{\alpha_{p,i,s} M_{p,h,i,s}^{0.75}}{Ef_p} \quad (1)$$

Where the subscripts for the model are: predator p , predator age i , sex s , that originated from area h , and occupies location j during year y time-step t , and prey on Chinook salmon of age a . The mass-at-age ($M_{p,h,i,s}$; kg) for killer whales⁵⁰, harbor seals⁵³, and California sea lions⁵⁴ and Steller sea lions⁵⁵ are all based on published estimates in the literature. The bioenergetics constant in the power function is assumed to be 0.75 for all predators⁵⁶. We used an average digestive efficiency (Ef_p) of 0.875^{48,51} for California and Steller sea lions, 0.825 for harbor seals⁵¹, and 0.847 for killer whales⁵⁰. The model also assumes that the predators consumed the entire Chinook salmon, regardless of size.

Selectivity ($SEL_{p,j,t,a}$) and fraction of energy comprised of Chinook salmon ($FEC_{p,j,t}$) for predators were based on a search of over 300 peer-reviewed journals and scientific reports³³, and updated in 2017 with additional publications and technical reports as indicated in the Appendix. Selectivity describes the size classes of salmon consumed by each predator species, and is relevant because a juvenile Chinook salmon has about three orders of magnitude less energy than the average adult Chinook salmon⁹. Fraction of energy comprised of Chinook salmon ($FEC_{p,j,t}$) would ideally be based on diet composition by percent energy or percent weight. However, the majority of the diet composition information for pinnipeds in the literature is based instead on frequency of occurrence (FO) observations, which is problematic because FO data do not sum to one, and many studies reporting FO do not partition salmon to species level. To transform pinniped FO into split sample frequency of occurrence (SSFO), a more useful proxy because the diet fractions sum to one, we used paired observations between FO and SSFO in Thomas *et al.*¹⁵. To disaggregate observations of total salmon consumed into Chinook salmon and other salmonids, we assumed the ratio of Chinook salmon to other salmonids from available species-specific harvest data in each area. This is a reasonable assumption since pinnipeds are considered to be generalist predators that are likely to select salmon species in proportion to the numbers present.

Salmon production, timing and distribution. Our model uses a monthly time-step t to track the number of Chinook salmon of age a in location j that originated from area h based on the attributes of run type r and origin o . The production of the Chinook salmon for a particular cohort ($S_{h,j,r,o,m,y,t,a=1}$) in the model is based on the annual smolt production ($R_{h,r,o,y}$) reported in the Regional Mark Information System database⁵⁷ for hatchery fish, and spawner escapement estimates from agency reports²⁷ for naturally spawning fish. Natural smolt production was estimated to be the spawner abundance, divided by two to yield female spawners, then multiplied by the average number of smolts produced-per-female Chinook salmon. There are very limited data on the smolts produced-per-female, and they are highly variable both within and between area tributaries (see review in supplemental material): we assumed an average of 220 smolts produced per female across all years and areas. The timing of juvenile Chinook salmon emigration from freshwater to the marine environment was based on hatchery release coded-wire-tag (CWT) information in the RMIS database. We assumed that hatchery and natural origin fish had the same migration timing for a given run type. We also assumed that the average lag between release date and their arrival in the near-shore areas was less than a month: that is, the month that a juvenile was released was the month that it entered the ocean.

The size of the juvenile Chinook salmon is important in estimating the number of juveniles consumed. Not only do juveniles grow during their down river migration, but they also grow during the occupancy in each area (areas A-H, Fig. 1) which can last for several months⁵⁸. Although our model consists of monthly time-steps related to predator consumption, tracking monthly cohorts of juvenile salmon from each of the tributaries along the eastern Pacific is beyond the scope of this analysis. We assumed that the average juvenile spends 10 days migrating down river and an additional one month (30 days) in each area. To account for this period of growth we assumed the average juvenile grows 1.0 mm/day⁵⁹, thus adding an additional 40 mm of length to the average juvenile release size. To account for variability in juvenile size, we assume the juvenile lengths are log-normally distributed with a standard deviation of 0.5 in our sensitivity analysis.

Predator-prey dynamics. The combination of predator and prey movement, as well as both natural and predation mortality, make the order of operations within a time-step important. From the Chinook salmon's perspective, the order in each time-step is as follows: 1) Chinook salmon distribute themselves across the areas based on the spatial transition matrix, followed by 2) natural mortality, 3) predation mortality, and finally 4) escapement. The number of Chinook salmon at the beginning of each time-step (S) is equal to the total abundance of wild and hatchery salmon at the end of the previous time step (S'), times the fraction of Chinook salmon from area h that are distributed to location j ($\Theta_{h,j,r}$),

$$\begin{aligned} S_{h,j,r,o,m,y,t,a} &= \Theta_{h,j,r} \sum_j S''_{h,j,r,o,m,y,t-1,a}, & t > 1, a > 0 \\ &= \text{MAT}_{h,r,o,m,a} \sum_j S''_{h,j,r,o,m,y-1,nt,a-1}, & t = 1, a > 0 \end{aligned} \quad (2)$$

The spatial transition matrix, $\Theta_{h,j,r}$, is based on Weitkamp²⁸ and describes the recovery location for tagged hatchery Chinook salmon in commercial and recreational fisheries throughout the eastern Pacific. The migratory state (m) of a Chinook salmon in a particular age class is determined at the beginning of the year ($t = 1$) and describes the conditional probability of a Chinook salmon maturing at age a ($\text{MAT}_{h,r,a}$) based on the Fishery Regulation Assessment Model (FRAM;⁶⁰). When a Chinook salmon changes from an immature to a mature state, it remains in that state throughout the year. Escapement refers to the mature salmon that leave the ocean pool to return to spawn in the natal tributaries. The number at the end of the time-step is equal to the number of salmon after predation (S') minus the escapement,

$$S''_{h,j,r,o,m=2,y,t,a} = S'_{h,j,r,o,m=2,y,t,a} (1 - \text{ESCT}_{j,r,t}), \quad t < nt \quad (3)$$

where, $\text{ESCT}_{j,r,t}$ is the fraction of the mature ($m = 2$) population leaving marine waters in that time-step. The average escapement timing was based on the summaries of west coast Chinook salmon populations⁶¹: escapement timing was assumed to vary by run type, but not area or year.

The number of Chinook salmon remaining after predation is equal to number at the beginning of the time-step times natural survival, which accounts for factors such as disease and consumption by predators not explicitly considered here, ($\text{surv}_{t,a}$), minus the number consumed by predators ($\text{NC}_{p,h,j,r,o,m,y,t,a}$),

$$S'_{h,j,r,o,m,y,t,a} = \text{surv}_{t,a} S_{h,j,r,o,m,y,t,a} - \min\left(\sum_p \text{NC}_{p,h,j,r,o,m,y,t,a}, 0.95 \text{surv}_{t,a} S_{h,j,r,o,m,y,t,a}\right) \quad (4)$$

The proportion surviving, $\text{surv}_{t,a}$, was assumed to vary by age and time-step⁶⁰, but not by run, origin, year, or migratory state. To avoid instances where the total consumption across all predators may exceed the available numbers of Chinook salmon, we assumed that the maximum consumption rate was 95%. The predation mortality is defined as,

$$\text{NC}_{p,h,j,r,o,m,y,t,a} = \frac{\sum_s \sum_i \text{ED}_{p,h,j,y,t,s,i,a}}{\text{EC}_{h,r,o,t,a}} \text{FS}_{p,h,j,r,o,y,t,m,a} \quad (5)$$

where, the number of Chinook salmon consumed ($\text{NC}_{p,h,j,r,o,m,y,t,a}$; d^{-1}) was based on: 1) the amount of energy derived from Chinook salmon ($\text{ED}_{p,h,j,y,t,s,i,a}$; kcal d^{-1}), 2) the energetic content of an individual Chinook salmon from a particular cohort ($\text{EC}_{h,r,o,t,a}$; kcal) which is a function of length-at-age throughout the year⁶⁰, and 3) the relative abundance of Chinook salmon cohorts in area j during time-step t ($\text{FS}_{p,h,j,r,o,y,t,m,a}$). Energetic content of Chinook salmon⁶² varies by length but not by sex. Relative abundance of Chinook salmon cohorts in area j during time-step t is computed as:

$$\text{FS}_{h,j,r,o,y,t,m,a} = \frac{S_{h,j,r,o,y,t,m,a}}{\sum_h \sum_r \sum_o \sum_y \sum_t \sum_m S_{h,j,r,o,y,t,m,a}} \quad (6)$$

Sensitivity analysis. We conducted a sensitivity analysis using Monte Carlo simulations to draw random deviates for four model inputs or parameters that affect both the biomass and numbers of Chinook salmon consumed: pinniped abundance (N), Kleiber multipliers (α), diet fraction (FEC), and salmon condition factor ($CCOND$; the intercept parameter of 0.000011 in O'Neill *et al.*'s⁶² formula relating fish length to energetic content). We also tested sensitivity to two parameters that affect only the calculation of the number of Chinook salmon consumed: fraction of Chinook salmon in the pinnipeds diets that are juveniles (SEL) and the length of the juveniles when they enter the ocean areas ($SMTL$). We did not vary killer whale abundance, since it is known with near perfect detection^{42,45,63}, and we did not vary the fraction of juvenile Chinook salmon in killer whale diets (killer whales do not consume juveniles).

Random deviations from the mean input values were assumed to be log-normally distributed for all the variables with a standard deviation of 0.1 on the log-scale for variables related to both biomass and numbers of Chinook salmon consumed (N , FEC , $CCOND$), a standard deviation of 0.05 for the activity multiplier (α), and a standard deviation of 0.5 on the log-scale for inputs related to strictly numbers consumed (SEL and $SMTL$). The random deviates for FEC and SEL were constrained to be between zero and one. Within a simulation the same deviate was applied to all values for a particular model input. For instance, the pinniped abundance (harbor seals, California sea lions, and Steller sea lions) would all deviate by the same proportion, and similarly, the diet fractions would all deviate by another proportion.

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Acknowledgements

We thank Chris Harvey, Lynne Barre, Jameal Samhour, and the anonymous reviewer for reviewing versions of this manuscript. We wish to thank Laurie Weitkamp for her help with the salmon distribution estimates and Michelle Rub for her results related to the Columbia River Chinook salmon consumption estimates. This work was supported by the Pacific Salmon Commission through the funded project “A spatially-explicit ecosystem model for quantifying marine mammal impacts on Chinook salmon in the Northeast Pacific Ocean”.

Author Contributions

Writing and edits to the dozens of drafts: All authors contributed significantly to the writing and rewriting of this manuscript. Predator diet and spatial distribution information: A significant part of this research was synthesizing years of diet data and determining the location of the predators throughout the year: Isaac C. Kaplan, Austen C. Thomas, Alejandro Acevedo-Gutiérrez, Dawn P. Noren, Michael J. Ford, M. Bradley Hanson, Jonathan Scordino, Steve Jeffries, Kristin N. Marshall, Andrew O. Shelton, Craig Matkin, Brian Burke, Eric J. Ward. Salmon spatial distribution data: In addition to the predator spatial distribution, determining the location of the salmon was a key part of the analysis: Brandon Chasco, Isaac C. Kaplan, Andrew O. Shelton, Brian Burke, Eric J. Ward. Model structure: The bioenergetics modeling was led by: Brandon Chasco, Isaac C. Kaplan, Austen C. Thomas, Alejandro Acevedo-Gutiérrez, Dawn P. Noren, and Eric J. Ward. Plotting and sensitivity analysis: Brandon Chasco, Isaac C. Kaplan, Austen C. Thomas, Kristin N. Marshall, Andrew O. Shelton, Eric J. Ward.

Additional Information

Supplementary information accompanies this paper at <https://doi.org/10.1038/s41598-017-14984-8>.

Competing Interests: The authors declare that they have no competing interests.

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ORIGINAL ARTICLE

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Demographic changes in Chinook salmon across the Northeast Pacific Ocean

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Funding information

Cook Inlet Salmon Disaster Technical Committee through the Pacific States Marine Fisheries Commission

Abstract

The demographic structure of populations is affected by life history strategies and how these interact with natural and anthropogenic factors such as exploitation, climate change, and biotic interactions. Previous work suggests that the mean size and age of some North American populations of Chinook salmon (*Oncorhynchus tshawytscha*, Salmonidae) are declining. These trends are of concern because Chinook salmon are highly valued commercially for their exceptional size and because the loss of the largest and oldest individuals may lead to reduced population productivity. Using long-term data from wild and hatchery populations, we quantified changes in the demographic structure of Chinook salmon populations over the past four decades across the Northeast Pacific Ocean, from California through western Alaska. Our results show that wild and hatchery fish are becoming smaller and younger throughout most of the Pacific coast. Proportions of older age classes have decreased over time in most regions. Simultaneously, the length-at-age of older fish has declined while the length-at-age of younger fish has typically increased. However, negative size trends of older ages were weak or non-existent at the southern end of the range. While it remains to be explored whether these trends are caused by changes in climate, fishing practices or species interactions such as predation, our qualitative review of the potential causes of demographic change suggests that selective removal of large fish has likely contributed to the apparent widespread declines in average body sizes.

KEYWORDS

age composition, climate, fishing, population demography, predation, size-structure

1 | INTRODUCTION

Populations respond to a variety of natural and anthropogenic factors that alter their dynamics and demography. The age-structure and size-structure of populations are responsive to environmental conditions, harvesting by humans, fluctuations in population density, diseases and species interactions such as predation, via changes in individual growth and size-dependent mortality. Intense harvesting can lead to age-truncated or juvenescent populations and thus reduced average sizes (Anderson et al., 2008; Hutchings & Baum, 2005; Sharpe & Hendry,

2009), climate warming has been suggested to cause widespread declines in organism body sizes (Gardner, Peters, Kearney, Joseph, & Heinsohn, 2011; Sheridan & Bickford, 2011), and it has long been recognized that changes in the age-structure or size-structure of a population can result from size-selective predation (Ebenman & Persson, 1988; Werner & Gilliam, 1984) as well as from shifts in competitive interactions within and between species (Jenkins, Diehl, Kratz, & Cooper, 1999; Walters & Post, 1993). Ultimately, the age and size demographics of a population are determined by the complex interactions among these factors, because they typically experience multiple stressors simultaneously.

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Chinook salmon is the largest and most highly valued species of Pacific salmon in North America. This anadromous species is native to the sub-arctic North Pacific Ocean and adjacent freshwater habitats. Chinook salmon are caught in recreational, commercial and subsistence fisheries and are preyed upon by a diverse group of predators, including iconic birds and mammals such as bald eagles (*Haliaeetus leucocephalus*), brown bears (*Ursus arctos*) and killer whales (*Orcinus orca*). Previous work and anecdotal knowledge suggest that the average size and age of Chinook salmon returning to their natal rivers have declined in recent decades. In particular, the oldest and largest fish seem to be disappearing from many populations. For instance, studies on Alaskan Chinook salmon have shown consistent decreases in the average size at return along with declining proportions of the oldest age classes, especially ocean age-4 fish (Kendall & Quinn, 2011; Lewis, Grant, Brenner, & Hamazaki, 2015). Similar trends towards declining mean weights of Chinook salmon caught in commercial fisheries along the west coast of North America were reported a few decades ago (Bigler, Welch, & Helle, 1996; Ricker, 1981), yet the causes of declining mean weight in the catch remained elusive. Furthermore, there has been no systematic assessment of the degree to which these changes in age-structure and size-structure are expressed across the native North American range of Chinook salmon, from California to western Alaska. Reductions in the average size of Chinook salmon are of concern because the loss of the oldest and largest individuals from a population can cause reduced population productivity, destabilize populations and negatively affect the long-term viability of Chinook salmon fisheries (Calduch-Verdiell, MacKenzie, Vaupel, & Andersen, 2014; Healey & Heard, 1984; Hixon, Johnson, & Sogard, 2014; Schindler et al., 2013).

A critical step towards understanding the causes of changes in Chinook salmon age-size structure is to identify whether changes in the overall mean length or weight result from changes in size-at-age, age composition or both. In addition, while each population may exhibit specific life history characteristics and face particular challenges with respect to environmental change and human impacts, understanding the spatial patterns of changes in age-structure and size-structure may provide key insights for understanding the most important causes of demographic change. Here, we examine changes in the size-at-age (length in mm) and age composition (ocean ages) of Chinook salmon along the west coast of North America over the past four decades. Specifically, we characterize common trends in size-at-age and age composition over time, identify important spatial patterns along the coast, and discuss previously suggested and novel hypotheses about the potential causes of demographic changes in Chinook salmon in the light of our findings.

2 | MATERIAL AND METHODS

2.1 | Chinook salmon ecology

The geographic distribution of Chinook salmon historically ranged from southern California to western Alaska and from northern Japan to north-east Siberia (Healey, 1991). Chinook salmon are anadromous and hatch and rear in freshwater, migrate to the ocean for most of their

life and return to their natal rivers to spawn (Quinn, 2005). Juvenile Chinook salmon typically spend 0, 1 or 2 years in freshwater before emigrating to the marine environment. Once in the ocean, many populations migrate thousands of kilometres northward along the west coast of North America, and populations from western Alaska migrate into the Bering Sea. However, the marine distribution patterns of Chinook salmon differ by region of origin, and some populations exhibit more local marine distributions, especially those from Puget Sound, southern Oregon and California (Weitkamp, 2010). The fish spend one to 5 years in the ocean to feed and gain most of their body mass before returning to their natal streams to spawn and then die. Northern populations tend to spend more time at sea (Quinn, 2005).

2.2 | Size and age time-series data

2.2.1 | Data sources

We gathered Chinook salmon size and age data from three different databases. First, coded-wire tag data were downloaded from the Regional Mark Information System (RMIS, www.rmis.org), a database of the Pacific States Marine Fisheries Commission (PSMFC), which contains release and recovery data for marked hatchery populations along the coast, from California to Alaska (note that RMIS contains some non-marked double index tags, i.e., tags used on fish without clipping the adipose fin). Our data set contained a total of 73 hatchery populations covering the time period 1977–2015. Second, data of wild (and hatchery) Chinook salmon returning to the Columbia River system were obtained from the Age and Scales database of the Washington Department of Fish and Wildlife (provided by D. Warren, WDFW). This data set contained six wild populations and catch records for the time period 1983–2011. Third, a data set with age and size information for wild Chinook salmon from Alaska was obtained from the Alaska Department of Fish and Game (ADFG; Lewis et al., 2015). The data set contained 10 wild populations and covered the time period 1977–2015. Fish age for all three data sets was estimated from scales. The grouping by river or watershed was determined by data availability, and while some of these groups are managed as “stocks,” we refer to all groups as “populations.”

The complete data set for our analyses contained a total of ~1.5 million individual measurements for 85 Chinook salmon populations with ocean-entry locations along the west coast of North America (Table S1; Figure 1). While this data set covers the North American range of the species, from western Alaska to northern California, many more populations exist that are either not monitored or for which data were not available, especially wild populations. Wild populations in our data set originate from western/south-central Alaska and from the Columbia River, whereas hatchery populations cover most of the range, from northern California to south-central Alaska.

2.2.2 | Data manipulation

Release and recovery data of hatchery populations from the RMIS database (California, Oregon, Washington, British Columbia and

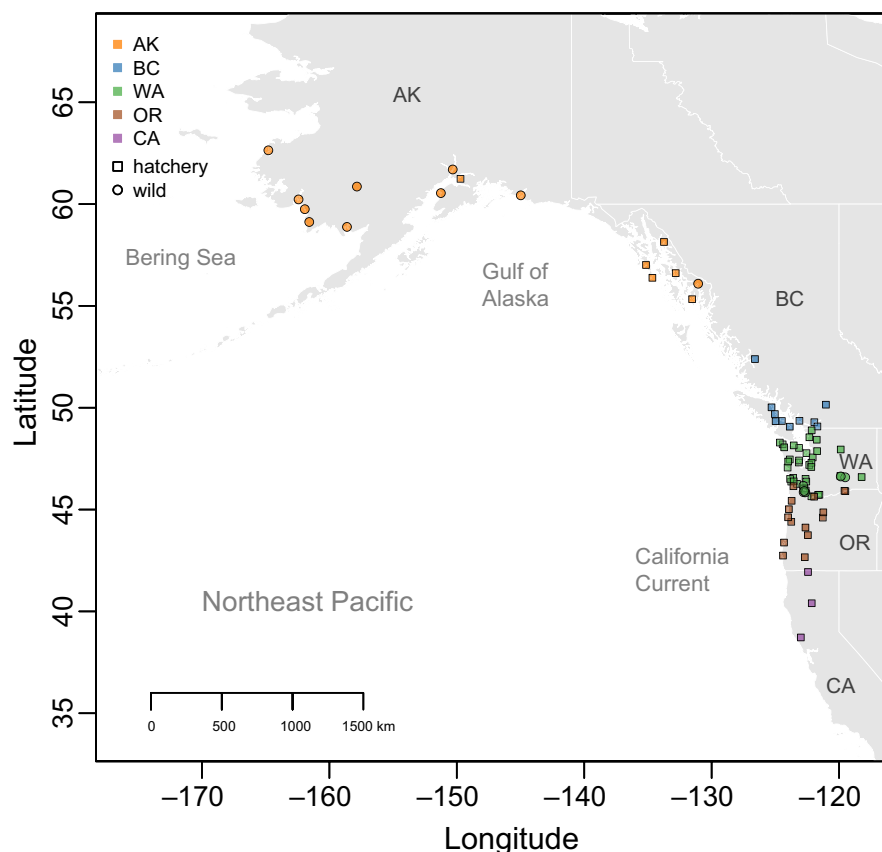


FIGURE 1 Map of study area. Shown are all wild (circles) and hatchery (squares) populations included in the analyses coloured by state/province: Alaska (orange), British Columbia (blue), Washington (green), Oregon (brown) and California (purple). Large marine ecosystems along the west coast of North America are indicated (East Bering Sea, Gulf of Alaska and California Current)

Alaska) were combined using individual tag codes or release IDs. Release groups with specific comments as well as all individuals caught in “Juvenile Sampling” or “High Seas” fisheries were not used in the analyses. Troll fisheries included in the data set catch a small proportion of Chinook salmon that would not have matured in the year of capture. This proportion was assumed to be constant through time. Columbia River populations from the WDFW database were categorized into *wild*, *mixed* and *hatchery* populations, and only those marked as wild were used in the analyses (six populations). Individual measurements smaller than 100 mm and larger than 1,500 mm were assumed to be misreported and excluded from the analysis. Populations with five or fewer years of data were also excluded. For wild populations, fishery information was converted to the RMIS fishery codes to allow fitting common models including hatchery and wild fish. Data with body length measured as snout to fork (SNF) and mid-eye to fork (MEF) were used. MEF lengths (~7.5% of data) were converted to SNF using an empirical formula: $SNF = 1.101MEF - 15.878$ (Pahlke, 1989), while other length codes were dropped from the analysis (<0.7% of data).

2.2.3 | Size and age metrics

Analyses of changes in size-at-age and age composition were based on the ocean age of the fish (i.e., the number of years a fish spent in marine waters). For example, a fish spending 4 years at sea and having four winter annuli in the ocean zone of the scale was designated as “ocean-4.” We included ocean ages 1–5 in the analyses,

with ocean ages 2–4 being the most frequently observed in our data set. Ocean-5 fish are rare in many populations, especially south of Alaska. Ocean-1 fish might be selected against by some of the fisheries and sampling methods used for capture. Age determination of Chinook salmon from scales is known to have observation error, but the accuracy of scale age data is typically about 90% (McNicol & MacLellan, 2010).

2.3 | Statistical approaches for quantifying changes

We used three different complementary approaches for assessing the temporal and spatial patterns in size-at-age and age composition of Chinook salmon populations along the coast: (i) multinomial logistic regression (MLR) was used to investigate temporal trends and spatial patterns in age composition, (ii) linear mixed effects (LME) modelling was used to identify coast-wide time trends in the size-at-age, and (iii) dynamic factor analysis (DFA) was used to model the spatial patterns of changes in the size-at-age as well as in the mean age of the populations. These approaches are explained in detail below.

2.3.1 | Multinomial logistic regression

To evaluate support for coast-wide trends in the age composition of Chinook salmon, we analysed fish recovery data using a hierarchical Bayesian MLR model (Hosmer, Lemeshow, & Sturdivant, 2013). In this framework, covariates (time) can be linked to latent proportions,

that is age composition, where the observed data are multinomial counts. Only populations with at least 10 years of data were included in the analysis. Univariate logistic regression estimates effects of covariates on an observed binary response, using a logit link function. Multinomial logistic regression extends this model to a multivariate setting, where individual fish may be assigned to one of five age classes.

The probability of a sampled fish being of age a from population p in time t was modelled using a logit link with corresponding probabilities $\text{logit}(\hat{p}_{a,t,p}) = \frac{\exp(B_{0,a,p} + B_{1,a,p} \cdot t)}{1 + \sum_{a=1}^4 \exp(B_{0,a,p} + B_{1,a,p} \cdot t)}$. For identifiability, we used ocean-5 fish as a reference group for all populations, setting $\exp(B_{0,5,p} + B_{1,5,p} \cdot t) = 1$. Because interpretation of model output is relative to the reference group, changing the reference group does not change the model results. The intercept terms, representing age compositions unique to each population in the first year of the data set, were assigned a Dirichlet prior with equal densities (uniform on the simplex), $B_{0,a=1:5,p} \sim \text{Dir}(\mathbf{1})$. Tests showed that results were insensitive to the choice of densities of the Dirichlet prior. Priors were assigned independently to each population such that no grouping was implied a priori by this choice. Because we are interested in population-specific, as well as global trends in age composition, the temporal slope terms were modelled hierarchically. The slopes were assumed to be drawn from a common distribution for each age, such that $B_{1,a,p} \sim N(\mu_a, \sigma_a)$, where μ_a and σ_a represent the mean and standard deviation of slopes for age a , in logit space. Finally, we used a multinomial observation model to link observed counts to predictions. For each individual, fish i recovered in time t from population p , this can be expressed as $Y_{i,t,p} \sim \text{Multinomial}(\hat{p}_{a=1:5,t,p}, N = 1)$.

We implemented the Bayesian multinomial regression model in STAN (Stan Development Team, 2016a) run via the R package *rstan* (Stan Development Team, 2016b). For each ocean age model, three MCMC chains were run for 4,000 iterations following a warm-up period of 1,000 iterations (no thinning). We examined model convergence using the effective sample size, Rhat, and by monitoring chains for divergent transitions using trace plots.

Based on model-predicted population-specific age proportions in each year, we calculated the relative change in the median proportions between the beginning and the end of the assessed time series for each population. The relative change was calculated as the difference between the average proportions in the two 5-year periods from 1979 to 1983 and 2001 to 2005 (brood years), thus covering a time period with complete age observations for most populations.

2.3.2 | LME models

We used a LME approach to model the size-at-age of Chinook salmon based on individual-level observations ($n = \sim 1.5 \times 10^6$) covering the brood years 1975–2009. Hence, data were not aggregated for this analysis. We fit linear mixed models to data for each age class of interest (ocean ages 1–5), where the response variables (length in mm) were normally distributed. The models were fit using the package *nlme* (v.3.1-128, Pinheiro & Bates, 2010) in R (v.3.3.2, R Core Team, 2016).

The initial model contained all explanatory variables, including year (up to 35 levels), rearing type (two levels: hatchery and wild), fishery (up to 38 levels), freshwater age (three levels: ages 0, 1 and 2), run type (five levels: spring, summer, fall, late fall and upriver bright) and sex (three levels: male/female/unknown) as factors, and day of year of sampling as continuous variable. The term “fishery” here refers to the fishery codes used by RMIS (see Table S1). The number of categories for some of the factors varied slightly between age-groups due to differences in data availability, that is few samples in that category for a given age-group. Categories with at least 25 observations were included in the analysis. It should be noted that sex may be estimated with unreliable external characteristics in ocean-phase fish (Lewis et al., 2015). We therefore fit the same mixed effects model without sex as a factor to confirm that our conclusions would not change. We also fit the same models based on escapement data only (as defined by the RMIS fishery group) to ensure that the conclusions would not depend on the inclusion of potentially selective fishery data.

An interaction between year and rearing type was included to test for different time trends in size-at-age between hatchery and wild fish. An interaction between year and state was not included due to missing observations for several year-state combinations. Random intercepts for each year nested within population were used to account for the lack of independence of the data within years and populations. We tested for the inclusion of nested random effects by comparing models with and without random effects using a likelihood ratio test and AIC model selection. Based on preliminary model runs without variance structure and subsequent visual analysis of the residuals for homogeneity of variances, we also tested for the inclusion of weights by year or population. We fit models of the following form: $L_i = \beta_0 + \beta_1 \text{FE}_1 + \dots + \beta_n \text{FE}_n + b_{p|y} + \epsilon_i$, where β_0 is the intercept, β_1, \dots, β_n are regression coefficients of the various fixed effects (FE), $b_{p|y}$ is a normally distributed random effect for year (y) nested in population (p) $\sim N(0, \sigma_b^2)$ and ϵ_i is a normally distributed error term $\sim N(0, \sigma^2)$.

The most parsimonious combination of fixed effects was determined using AIC based multimodel inference using the *MuMIn* package (v.1.15.6, Burnham & Anderson, 2002) by evaluating the complete set of models with all possible combinations of fixed effects. Models that differed in their random effects were compared using restricted maximum likelihood (REML), while models with different fixed effects structures were compared using maximum likelihood parameter estimation (ML). The final models were fit using REML.

2.3.3 | Dynamic factor analysis

To identify the spatial coherence in the temporal trends in size-at-age and age composition between regions, for example between states, we applied DFA, a multivariate time-series analysis approach (Zuur, Tuck, & Bailey, 2003). For this analysis, we constructed population-specific time series of mean age and mean size-at-age, that is using aggregated population-level time series that do not account for

differences in sample size (as opposed to the LME approach). Mean age was computed in brood years for which each age-group could have been observed. Only populations with at least 5 years of data were included in the analyses.

In DFA, the time series are modelled as a linear combination of hidden trends, which reflect the temporal variation shared among the time series, and population-specific error terms: $\mathbf{y}_t = \mathbf{Z} \mathbf{x}_t + \mathbf{v}_t$, where the hidden trends (\mathbf{x}_t) are modelled as random walk processes with a noise component (\mathbf{w}): $\mathbf{x}_t = \mathbf{x}_{t-1} + \mathbf{w}_t$. Matrix \mathbf{Z} contains factor loadings on the shared/hidden trends (\mathbf{x}_t), and $\mathbf{v}_t \sim \text{MVN}(\mathbf{0}, \mathbf{R})$ is the residual error, which is assumed to be multivariate normally distributed (MVN) with mean zero and variance-covariance matrix \mathbf{R} . The process noise $\mathbf{w}_t \sim \text{MVN}(\mathbf{0}, \mathbf{I})$ is assumed to be multivariate normally distributed with mean zero and variance-covariance matrix \mathbf{I} , which is the identity matrix such that the hidden trends are independent. The initial state vector is set to a mean of zero and a diagonal variance-covariance matrix with large variances. Because we were interested in the most common trend shared among the time series, we only fit one-trend models. We used a variance-covariance matrix (\mathbf{R}) with shared variances and no covariance among populations because preliminary tests using AIC model selection indicated *diagonal and equal* as the most parsimonious error structure for the mean size-at-age and mean age time series. Time series were z-scored (de-meaned and standardized) to account for differences in means and variances.

We implemented DFA in a Bayesian framework using an implementation of the model in STAN. Code to run the Bayesian DFA is available on GitHub: <https://github.com/nwfsc-timeseries/statss> (Ward, Scheuerell, & Holmes, 2018). For each ocean age model, we ran 10,000 iterations following a warm-up period of 10,000 iterations. We examined convergence across parameters using the effective sample size, Rhat, and monitoring chains for divergent transitions using trace plots. The Bayesian estimates corresponded to those generated by a DFA in a maximum likelihood framework using the package MARSS (Holmes, Ward, & Wills, 2012).

2.4 | Additional time-series data

To perform a qualitative review of the commonly hypothesized causes of changes in Chinook salmon age-size structure, we gathered time-series data on key indices such as overall fishing pressure,

the number of hatchery fish, climate variables and the number of marine mammal predators in the ocean. Specifically, we compiled data on total commercial catches and the number of hatchery releases of Chinook salmon in the North Pacific Ocean (www.npafc.org), coastal sea surface temperatures in summer (July–September) and winter (January–March) for a rectangle defined by latitudes 41.0°–54.3° north and longitudes 125.6°–135° west (data source: www.esrl.noaa.gov, Kalnay et al., 1996), ocean climate indices such as the PDO (Pacific Decadal Oscillation, <http://research.jisao.washington.edu>) and NPGO (North Pacific Gyre Oscillation, www.o3d.org/npgo), and the abundances of resident killer whales and other marine mammal predators (Chasco, Kaplan, Thomas, Acevedo-Gutiérrez, Noren, Ford, & Marshall, 2017; Chasco, Kaplan, Thomas, Acevedo-Gutiérrez, Noren, Ford, & Shelton, 2017). Killer whale numbers were based on abundances of Southern Residents (Center for Whale Research, 2017), Northern Residents (Ellis, Ford, & Towers, 2007), Southeast Alaska Residents and index pods of Gulf of Alaska Residents (Allen & Angliss, 2013). Missing years of data for Southeast Alaska and Gulf of Alaska Residents were interpolated using an annual growth rate of 2.9% (estimated average rate of increase in all non-Southern Residents).

3 | RESULTS

3.1 | Spatial and temporal patterns in age composition

The age composition of many of the Chinook salmon populations along the coast has changed considerably over the past few decades. Pronounced changes in age composition were found in Alaskan populations, where the proportions of younger ocean ages have increased and the proportions of older ocean age classes have decreased over time (Figure 2). In particular, ocean-5 fish that used to make up 3%–5% of the runs have become essentially non-existent (<0.5%) in recent years, and proportions of ocean-4 fish have also declined sharply. The declining trend in the proportions of older ocean ages is also apparent but slightly weaker in Washington, Oregon, and basically absent in California and British Columbia. Consequently, the overall mean age of all populations combined by state declined most significantly in Alaska, declined slightly in Washington, Oregon and California, and increased over time in British Columbia. These

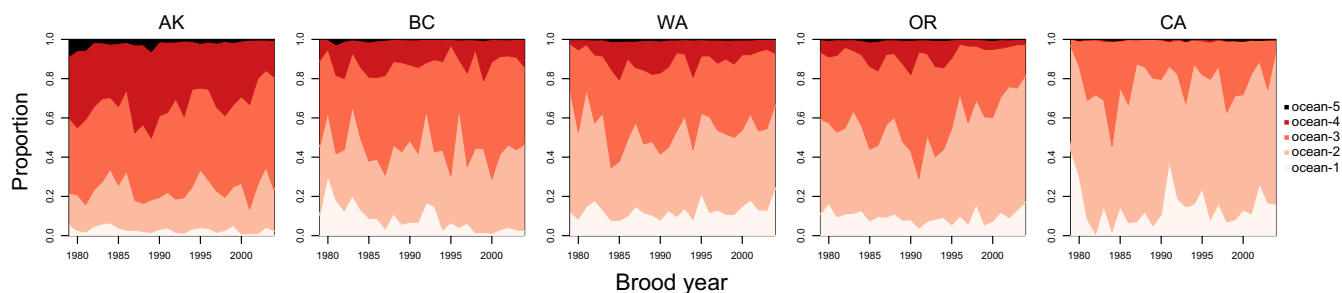


FIGURE 2 Age proportions of Chinook salmon by state/province. Shown are mean proportions of ocean-1 fish (bottom polygons, light red) to ocean-5 fish (top polygons, black) by brood year

same trends were highlighted by the DFA analysis. The most common trend in mean age shared among populations showed a relatively continuous decline over time (Figure 3). Most populations from Alaska, Oregon and Washington (except some of the wild populations) followed this trend of declining mean age, while most populations from British Columbia showed the opposite trend (i.e., mostly negative loadings on the DFA trend). Wild populations from Alaska followed the declining trend in mean age, similar to hatchery populations from Alaska, whereas the wild populations from Washington showed weaker associations with the declining trend (Figure 3).

The multinomial regression model further illustrated that the proportions of older age-groups are consistently lower in recent brood years (2001–2005) compared to the early period (1979–1983). In populations with ocean-5 fish, the proportion of this age-group

has consistently declined (Figure 4), and proportions of ocean-4 have also declined in over 75% of the populations examined coast-wide. While these findings suggest some shared temporal trends in the age proportions along the coast, our analysis also highlighted significant differences in age trends between regions, indicating region-specific factors affecting the age composition of Chinook salmon populations. The most substantial changes were found for Alaska, where proportions of ocean-2 and ocean-3 fish increased and those of ocean-4 and ocean-5 fish decreased in almost all populations (Figure 4). At the southern end of the distribution range, where the age-structure is generally shifted towards younger ocean ages, the loss of older individuals implies declining proportions of ocean-4 and often ocean-3 fish, especially in California. A clear latitudinal cline is therefore evident for ocean-3 fish, such that proportions of most

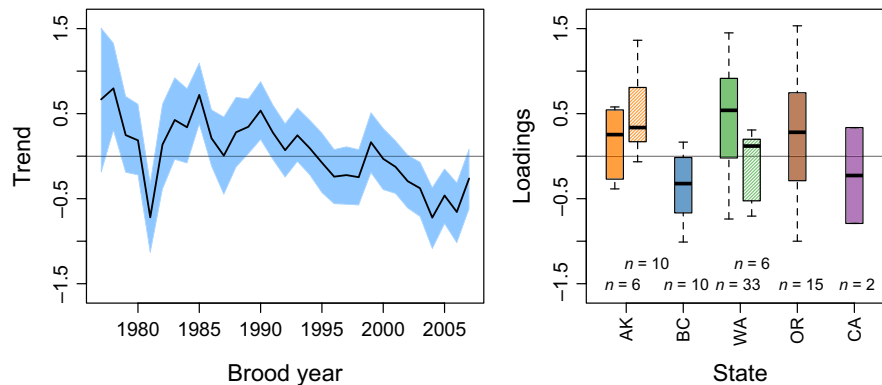


FIGURE 3 Dynamic factor analysis (DFA) of mean age of Chinook salmon along the west coast of North America. Common trend in mean ocean age of all populations by brood year (left) shown as medians (black line) with 95% credible intervals (blue bands). The right panel shows the loadings by each state/province on this common trend. Plots show median values (thick lines), 25th and 75th quartiles (boxes), and 1.5 times the interquartile range (whiskers, outliers omitted). Filled boxes indicate hatchery populations and shaded boxes indicate wild populations. The number of populations in each region is indicated at the bottom

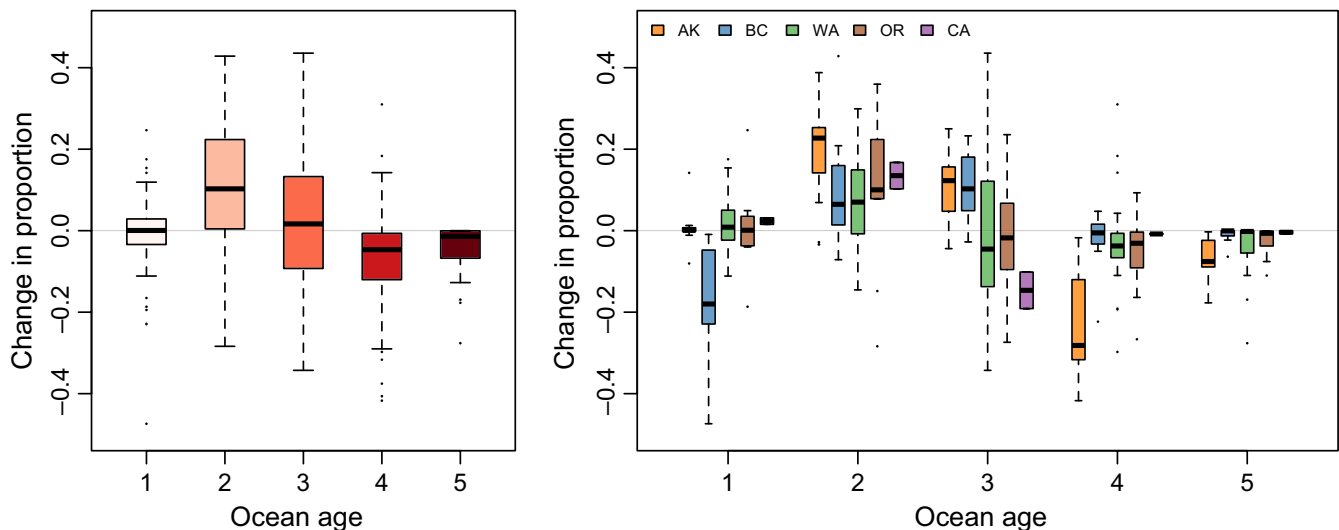


FIGURE 4 Coast-wide changes in age proportions of Chinook salmon along the North American west coast. Relative changes in the proportion of each ocean age between the early and late periods of the time series. Box plots are based on population-specific age proportions predicted by the multinomial logistic regression model and show median values (thick lines), 25th and 75th quartiles (boxes), 1.5 times the interquartile range (whiskers) and outliers (circles). Colours on the left indicate ocean ages 1–5 (light to dark red), and colours on the right refer to Alaska (orange), British Columbia (blue), Washington (green), Oregon (brown) and California (purple)

populations examined increased in Alaska and British Columbia, increased or decreased in Washington and Oregon, and decreased in California.

3.2 | Spatial and temporal patterns in size-at-age

Inclusion of a nested year-in-population random effect was supported in all five size-at-age models (one for each ocean age). Four of the five selected models included fixed effects for brood year, rearing type, fishery, freshwater age, run type and sex as factors, and day of year of capture as a continuous variable. The selected ocean-5 model, which contained the fewest data, did not include freshwater age and day of year, but otherwise had the same structure. In addition, the interaction between the fixed effects of year and rearing type (hatchery or wild) was not supported in the models with the exception of the ocean-1 model. Hatchery-origin and wild populations thus did not show significantly different temporal trends except for the youngest age class. The conditional R^2 values of the selected models for ocean ages 1–5 were 0.70, 0.51, 0.37, 0.45 and 0.56. Hence, the variance explained by the fixed and random effects was between 37% and 70%.

The year effects of the size-at-age models showed that the size of Chinook salmon across their entire North American range has varied greatly over the past four decades. All ocean ages from ocean-1 to ocean-5 show some year-to-year variation and clear temporal trends in size-at-age (Figure 5). The overall trend is that the size-at-age of ocean-1 and ocean-2 fish has increased, while the size-at-age of ocean-4 and ocean-5 (and to some extent ocean-3) fish has decreased over time. The increasing size trend of young fish was found in most hatchery populations, but was generally weaker or absent in wild populations, especially those from Alaska (see below). The size decline in ocean-4 and ocean-5 fish was found for almost all hatchery and wild populations and was most rapid during the recent 10–15 years (i.e., since about 2000). Our findings suggest that since the late 1970s, average sizes (lengths) have *increased* by about 7% and 3% for ocean ages 1 and 2, respectively, whereas sizes have *decreased* by about 5%, 7% and 9% for ocean ages 3, 4 and 5, respectively. The coast-wide decline in the size-at-age of older fish has occurred almost continuously over time, although some shorter periods of stable or increasing sizes have occurred (Figure 5). It is worth noting, however, that the nested year-in-population random effects suggest considerable among-population variation in the predicted sizes and the temporal trends in size-at-age (Figure S1).

Hatchery fish were generally larger at ocean entry and remained larger compared to wild fish up to ocean age-3 ($p < .0001$), but this size difference diminished throughout ocean residence, and average sizes were similar for ocean ages 4 and 5 ($p > .05$, Figure 6). On average, hatchery fish were more than 20% larger than wild fish at ocean ages 1 and 2. Similarly, freshwater age influences the size of ocean ages during the first three years at sea, but this difference weakened for ocean-4 and disappeared for ocean-5 fish (Figure S2). Day of capture had a positive effect in all ages, that is larger fish were caught later in the year, but this effect also continuously weakened from ocean age 1–5. The various run types showed only slight differences

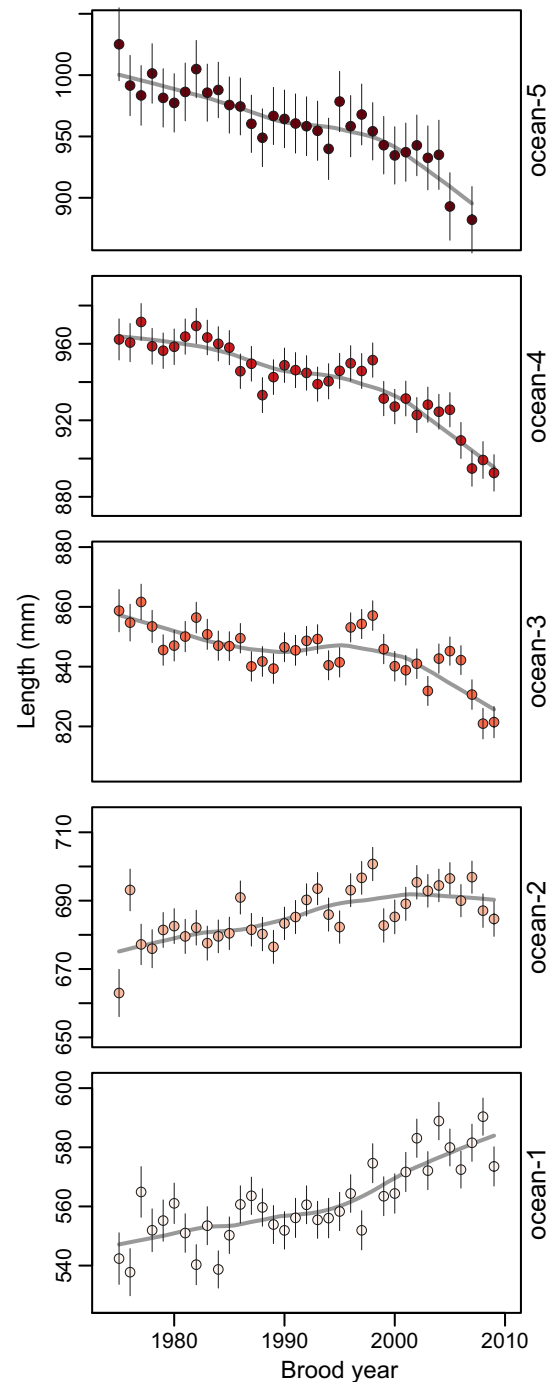


FIGURE 5 Linear mixed effects predictions of size-at-age for Chinook salmon across the North American west coast. Annual predictions for the size-at-age of each age-group (circles, with standard errors), from ocean-1 (bottom) to ocean-5 (top). The grey line illustrates the time trend in size-at-age (loess smoother with span=0.5). Year predictions were made by setting all other predictors to median values (continuous variables) or the most common category (factors) [Colour figure can be viewed at wileyonlinelibrary.com]

in size-at-age, with fall and summer runs being generally larger than spring runs. Finally, there was a significant effect of fishery on size-at-age, where the smallest Chinook salmon were caught in ocean

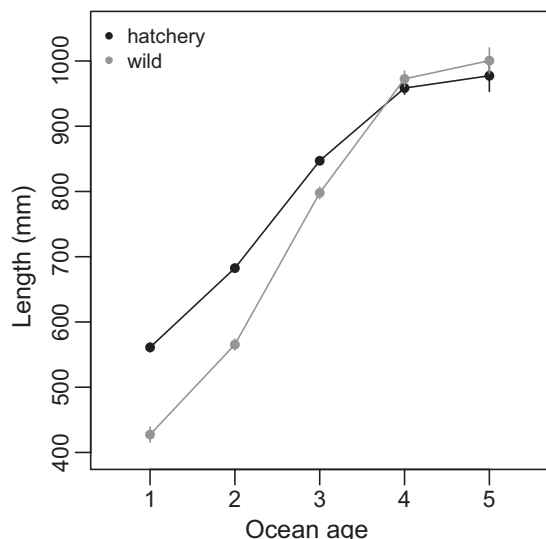


FIGURE 6 Hatchery vs wild Chinook salmon. LME predictions for the size-at-age of hatchery and wild Chinook salmon for each ocean age

troll fisheries and the largest fish were caught in escapement fisheries (in-river or terminal fisheries). The normalized residuals of the LME model showed some heterogeneity in residual variance, specifically a decrease in the residual variance over time for ocean ages 4 and 5 (Figure S3). Including this variance structure in the model, by allowing for different variances per year, did not change the model selection or predictions (but was computationally costly due to the large amount of length data).

The DFAs with one common trend for each ocean age across all populations extracted shared trends that closely matched the temporal trends described by the LME year effects (Figure 7). The dominant size-at-age trends were shared among many of the populations (by definition), yet some differences between regions and rearing types became apparent. For instance, most hatchery populations loaded strongly on the positive size trend of ocean age 1 and 2 fish, whereas most wild populations from western Alaska and several of the wild populations from the Columbia River did not follow this trend. Populations along the coast from western Alaska to northern Oregon loaded strongly on the declining size trend of ocean-4 fish, including wild and hatchery fish. In contrast, populations from southern Oregon and California as well as those from Puget Sound, a region with a higher proportion of populations that do not migrate far in the ocean, showed weak or even negative loadings on the dominant trends of ocean-4 fish and thus did not follow the declining size trend (Figure S4).

4 | DISCUSSION

4.1 | Changes in age-size structure

We found that the size-structure and age-structure of Chinook salmon have changed considerably across the Northeast Pacific

Ocean since the late 1970s. While changes in age proportions showed some region-specific trends, many of the populations coast-wide have experienced declines in the proportion of ocean-4 and ocean-5 fish, and proportions of ocean-2 fish have generally increased. Furthermore, the size-at-age of ocean-1 and ocean-2 has increased over time, at least in most hatchery populations, whereas the size-at-age of ocean-4 and ocean-5 fish has declined considerably, especially since about 2000. In addition to the temporal trends in age composition and size-at-age, our results also showed significant effects of other explanatory variables, including rearing type, fishery, freshwater age and run type. Hatchery-origin fish were found to be considerably larger than wild fish during the first 2 years of ocean residence, but this size difference disappears for older ocean ages, suggesting faster growth rates that lead to larger size-at-age early in life but similar maximum sizes.

Declining sizes of older ocean fish were found for both wild and hatchery Chinook salmon along the coast. Our spatial analysis of changes in size-at-age revealed that the dominant trends are remarkably consistent across the entire Northeast Pacific Ocean. Most populations along the northern and central part of the coast, from western Alaska through northern Oregon, follow the declining size trend of ocean-4 fish. Furthermore, populations from Southeast Alaska, British Columbia, coastal Washington and the Columbia River tend to follow the increasing size trend of ocean-1 and -2 fish. The difference between hatchery and wild Chinook salmon in Alaska for younger ocean ages could either result from different growth trajectories of hatchery vs. wild fish, consistently increasing release sizes of hatchery fish, or from differences between regions, because most of the hatchery populations were from Southeast Alaska, whereas the majority of wild populations were from central and western Alaska.

Previous work documented changes in Chinook salmon age-size structure in some of the regions analysed here. For instance, it was shown that the mean size (length) of some Chinook salmon populations in Alaska has declined by up to 10% since the early 1980s, concurrent with declines in mean age (Lewis et al., 2015). These authors also found that the size and age trends were consistent for data derived from commercial gill net fisheries and in-river weir counts. Similarly, the mean age of Chinook salmon returning to Nushagak River, western Alaska, as well as the size of the older fish, has declined in the same time period (Kendall & Quinn, 2011). Earlier studies had reported declines in mean weight of Chinook salmon caught in commercial fisheries in many regions of North America (Bigler et al., 1996; Ricker, 1981). Interestingly, the weight trends for British Columbia were not as continuous as for other regions (Bigler et al., 1996; Ricker, 1981), which is in line with a recent study showing that the weight of Chinook salmon caught in British Columbia fisheries has declined in the 20 years prior to the early 1970s, increased up to about 2000, and thereafter decreased again (Jeffrey, Côté, Irvine, & Reynolds, 2017). This pattern in the mean weight of the fish might be caused by changes in the age composition. Our results suggest that age trends of populations from British Columbia differ from those observed elsewhere. However, the trends in size-at-age of most

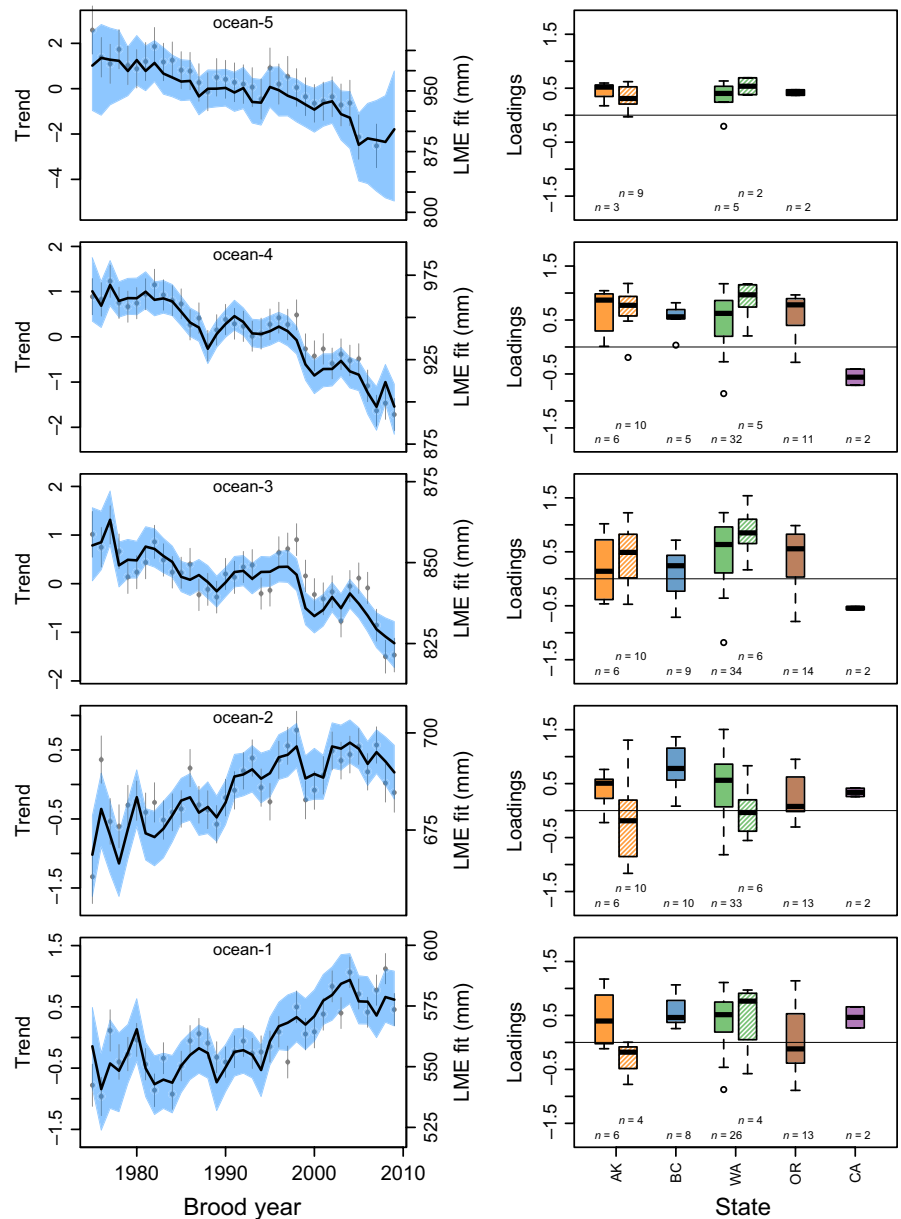


FIGURE 7 Dynamic factor analysis of size-at-age for Chinook salmon. Common trend in size-at-age among all populations (left) showing the median estimate (black line) with 95% credible intervals (blue bands), along with predictions from the LME (grey circles and error bars), as well as the loadings on the common trend clustered by region (right, ordered north to south) for ocean ages 1 (bottom) to 5 (top). Filled boxes indicate hatchery populations and shaded boxes indicate wild populations. The number of populations in each region is indicated at the bottom

populations from British Columbia are coherent with the size trends observed coast-wide.

Chinook salmon populations that spawn in north-east Asia, at least those in Kamchatka (Russia), seem to exhibit similar age and size trends as observed for North American populations (Bugaev et al., 2015; Popova, 2015). Specifically, long-term data series from the Bolshaya Vorovskaya River in south-western Kamchatka suggest that mean sizes and proportions of ocean-4 and ocean-5 fish have been declining since the late 1970s (Popova, 2015). These shifts in mean size and age closely resemble the trends reported here for North American populations, although it is not clear whether size-at-age has declined, or whether the negative trend in mean size resulted from shifts in age composition alone. Marine distributions of Russian Chinook salmon populations overlap with those of western and central Alaskan populations in the western parts of the Bering Sea and Gulf of Alaska (Larson et al., 2013).

4.2 | Consequences of demographic change

The loss of old and large individuals from a population can have important ecological and economic implications. Declines in the average size and age can cause a reduction in population productivity, because smaller salmon have lower fecundity and lower offspring survival, and may not be able to dig deep enough redds to reduce susceptibility to scouring (Healey & Heard, 1984; Hixon et al., 2014). Smaller fish could also reduce the transport of marine-derived nutrients into freshwater and terrestrial ecosystems (Moore et al., 2011; Schindler et al., 2003), unless abundances increase. Furthermore, a less diverse age-structure may decrease population stability through increased variability in abundance (Anderson et al., 2008; Hsieh et al., 2006) or weaker portfolio effects through reduced life history complexity (Schindler et al., 2010). Finally, due to their ecological importance and high social and market values, large fish are

of particular value to Chinook salmon fisheries, and an erosion of the age-size structure may negatively affect their long-term viability (Calduch-Verdiell et al., 2014; Healey & Heard, 1984).

4.3 | Potential causes of observed changes

The reported changes in the size and age distribution of Chinook salmon populations across the Northeast Pacific could be responses to a variety of factors. Commonly hypothesized causes of change in salmon age-size structure include (i) size-selective harvest, (ii) environmental change such as changes in temperature regimes or ocean productivity that affect growth and mortality rates, and (iii) impacts of hatchery practices and increased competition for food (including non-Chinook hatchery populations). A previously overlooked hypothesis attributes the observed changes to (iv) predation by marine mammals, especially a growing number of resident killer whales and their size-selective predation on Chinook salmon (Chasco, Kaplan, Thomas, Acevedo-Gutiérrez, Noren, Ford, & Marshall, 2017; Chasco, Kaplan, Thomas, Acevedo-Gutiérrez, Noren, Ford, & Shelton, 2017). In the following, we present these hypotheses in detail and discuss their qualitative consistency with the findings reported in this paper. A summary of data relevant for evaluating these hypotheses at a broad geographic scale is provided in Figure 8.

4.3.1 | Harvest

The loss of the oldest and largest fish, as described for several Chinook salmon populations, is commonly attributed to size-selective fishing. Previous work has suggested that size declines in Chinook salmon may be caused by sufficiently strong and selective fishing and the resulting evolutionary trait changes by showing that size-selective fishing could produce an evolutionary response towards smaller average sizes and ages of Chinook salmon within a few decades if exploitation rates and size selectivity are sufficiently strong (Bromaghin, Nielson, & Hard, 2011; Eldridge, Hard, & Naish, 2010; Hard, Eldridge, & Naish, 2009). In practice, it is difficult to evaluate whether the observed phenotypic change is caused by an underlying genetic response. The expected impacts of size-selective fishing are generally consistent with the observed pattern that fish return at smaller sizes and younger ages in many rivers and regions. However, size limits vary by state, selection curves vary among fisheries (e.g., troll, gillnet, subsistence and recreational fisheries) and fishery selectivity tends to be weak (e.g., Kendall & Quinn, 2011). While one may expect a lag in the demographic response of fish populations to fisheries selection, at least on the order of a few generations, most of the coastal fisheries were well developed by the 1970s, and exploitation rates have been declining since the 1990s (Hilborn et al., 2012; Figure 8). However, the decline in the size of ocean-4 + fish has accelerated since about 2000. Exploitation rates vary greatly among populations even within the same region (Lewis et al., 2015), yet most populations along the west coast, that is north of central Oregon, exhibit a common decline in size-at-age (Figure 7). Some of the populations have experienced relatively low harvest

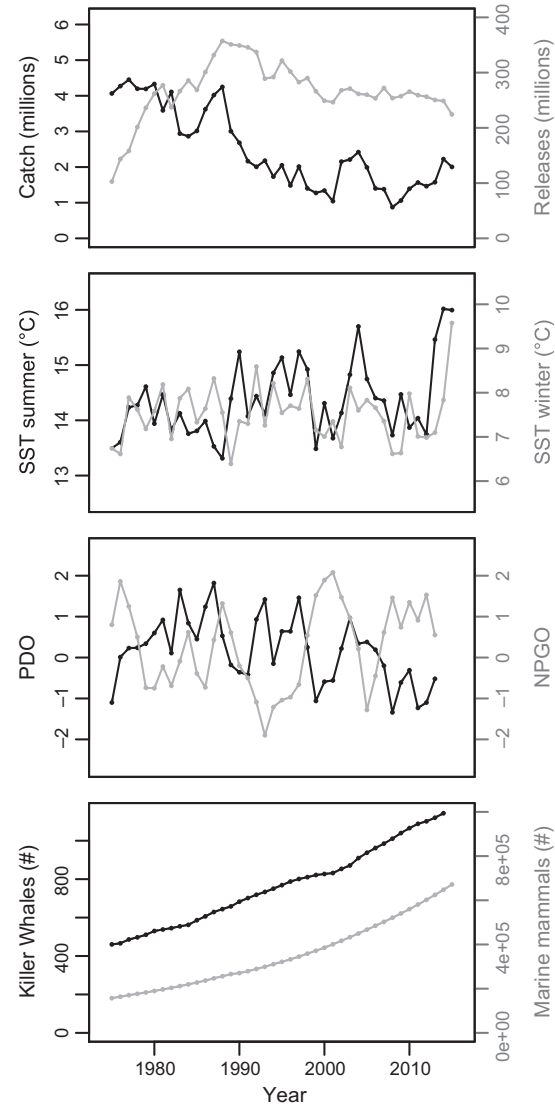


FIGURE 8 Annual indices of fishing pressure, hatchery releases, climate variation and predation. Shown are (a) total commercial catches and hatchery releases of Chinook salmon in the North Pacific Ocean, (b) coastal sea surface temperatures in summer and winter, (c) ocean climate indices PDO and NPGO, and (d) abundances of resident killer whales and other marine mammal predators. Black (left) and grey (right) y-axes apply to black and grey time series

rates (CTC, 2016; JTC, 2006). For example, exploitation rates of the Nushagak and Goodnews rivers populations are rather low (<40%) compared to those of other western and central Alaskan populations (>50%), for example the Yukon and Copper rivers, while the declining trends in size-at-age are similarly pronounced (Lewis et al., 2015).

4.3.2 | Hatcheries

Total hatchery releases of Chinook salmon into the Pacific Ocean increased substantially during the 1970s and somewhat during the 1980s and have since been declining (Figure 8). Hatchery-reared fish could alter the age-size structures of populations coast-wide via two

mechanisms: direct effects on competition for resources in the ocean (Ruggerone & Goetz, 2004), or as a consequence of selective breeding and introgression of selected genotypes into wild populations, especially small populations in close geographic proximity to hatcheries (Van Doornik et al., 2013). The selective breeding of Chinook salmon in hatcheries might have produced faster-growing fish that attain larger sizes during the first two or 3 years in the ocean but do not reach larger maximum sizes compared to wild fish. Alternatively, larger sizes of hatchery fish during the early ocean phase could be a result of the larger size at release from the hatcheries. Introgression of hatchery-reared fish might have contributed to increased size-at-age of ocean-1 and ocean-2 fish in wild populations. A larger size-at-age of young ocean fish may further contribute to a decrease in the proportion of older ocean ages at return if maturation is primarily determined by size. Nevertheless, these trends cannot explain the decline in size-at-age of ocean-4 and ocean-5 fish that is apparent in all wild populations, including many that are not exposed to hatchery strays. For instance, the trend of declining size-at-age of ocean-4 and ocean-5 fish is prevalent among wild populations in western Alaska that experience no introgression of hatchery genotypes because no Chinook salmon hatcheries currently operate in western Alaska (Stopha, 2017). The observed changes in size-at-age suggest that growth conditions for younger fish have improved (larger size of ocean-1 and ocean-2 fish), and the continuous decline in the size of older fish is not consistent with the hypothesized effect of increased intraspecific competition.

4.3.3 | Interspecific competition

Increased interspecific competition for food with other Pacific salmon is expected to be of minor importance, because older Chinook salmon feed at a higher trophic level than other species (Johnson & Schindler, 2008). While changes in growth can result from changes in food abundance or competition, our findings suggest that growth conditions for younger fish have actually improved and support increased growth rates, which is difficult to reconcile with general shifts in ocean productivity or carrying capacity. In addition, competition among Pacific salmon is believed to be most intense during the first two or 3 years of ocean life (Ruggerone & Connors, 2015). Negative effects of direct competition with other salmonids are therefore unlikely to be the driving mechanisms of declining size-at-age among older Chinook salmon. However, indirect effect of increasing abundances of other salmonids on the prey base of older Chinook salmon in the ocean, for instance through impacts on other life-stages of the prey that are not targeted by Chinook salmon or through more complex food web linkages, cannot be ruled out as a potential driver of changes in age-size structure.

4.3.4 | Environmental variation

Previous work on Chinook salmon suggests that changes in ocean temperature are not strongly linked to changes in growth and average size of adult fish (Ricker, 1981; Ruggerone, Nielsen, & Agler, 2009). While the faster life history with higher growth rate

and smaller maximum size could be a response to climate warming (Cheung et al., 2013; Gardner et al., 2011; Ohlberger, 2013; Sheridan & Bickford, 2011), temperatures in the coastal waters of the Northeast Pacific (Figure 8) have been highly variable with only weak increasing trends over the past few decades (Johnstone & Mantua, 2014). Ocean conditions in the Northeast Pacific are strongly linked to large-scale climate phenomena such as El Niño Southern Oscillation (ENSO), the North Pacific Gyre Oscillation (NPGO) and Pacific Decadal Oscillation (PDO). These climate indices are known to affect the survival and productivity of Pacific salmon in the ocean (Hare, Mantua, & Francis, 1999; Kilduff, Di Lorenzo, Botsford, & Teo, 2015; Mantua, Hare, Zhang, Wallace, & Francis, 1997; Ohlberger, Scheuerell, & Schindler, 2016), but their patterns of variability are most strongly expressed at the interannual and interdecadal time scales (Figure 8).

4.3.5 | Natural mortality

Changes in natural mortality, for instance due to predation by marine mammals, have so far been largely overlooked as a potential cause of changes in Chinook salmon age-structure and size-structure. Like fishing, predation may cause shifts in the size and age composition of populations via the removal of individuals and/or selection for different phenotypes such as faster growth and earlier maturation (evolutionary change). Marine mammals that prey on Chinook salmon include pinnipeds and cetaceans such as harbour seals (*Phoca vitulina*), Steller sea lions (*Eumetopias jubatus*), California sea lions (*Zalophus californianus*) and resident killer whales. Many of these predators have increased in abundance in coastal waters of the Northeast Pacific during the past decades, primarily due to harvest bans established since the 1970s by the US Marine Mammal Protection Act and the US Endangered Species Act (Magera, Flemming, Kaschner, Christensen, & Lotze, 2013). A recent study estimated that consumption of Chinook salmon biomass by marine mammals, including pinnipeds and killer whales, has nearly tripled since the mid-1970s (Chasco, Kaplan, Thomas, Acevedo-Gutiérrez, Noren, Ford, & Marshall, 2017; Chasco, Kaplan, Thomas, Acevedo-Gutiérrez, Noren, Ford, & Shelton, 2017). Predation by pinnipeds, however, is unlikely to cause declines in the average age and size of adult fish, because these predators mostly select large juvenile and small adults, do not show a preference for Chinook salmon compared to other salmonids and are mostly concentrated near river mouths (Adams et al., 2016; Thomas, Nelson, Lance, Deagle, & Trites, 2017).

Resident killer whales, on the other hand, selectively prey upon Chinook salmon, particularly the oldest and largest individuals (Ford et al., 1998; Hanson et al., 2010; Herman et al., 2005). About 90% of Chinook salmon eaten by residents are 4–6 years old (Ford & Ellis, 2006), and the abundance of resident killer whales has continuously increased since the 1970s (Matkin, Ward Testa, Ellis, & Saulitis, 2014; Ward et al., 2016). Currently, the total number of resident killer whales in the Northeast Pacific Ocean is estimated to be at least 2300 individuals (Muto et al., 2017), with many populations increasing 2–3× over the last 40 years. However, abundance estimates

are uncertain for resident killer whales inhabiting the Bering Sea and coastal waters along the Aleutian Islands.

Bioenergetics calculations suggest that the residents currently inhabiting the coastal waters between northern California and southern Alaska (not including those along the Aleutian Islands and in the Bering Sea) consumed roughly 10^4 metric tons of Chinook salmon in 2015, which is ~70% of the total marine mammal consumption by weight (Chasco, Kaplan, Thomas, Acevedo-Gutiérrez, Noren, Ford, & Shelton, 2017). This is equivalent to an annual consumption of about 2.3 million adult-sized Chinook salmon, and similar to the recent annual commercial catch in the North Pacific Ocean (~2 million Chinook salmon, Irvine et al., 2009). While the relative contributions of harvest and natural predation vary by population and region, total coast-wide mortality of Chinook salmon has increased over time despite reductions in fishery harvest. Chinook salmon are exposed to predation by resident killer whales along the coast, and exposure to predation during ocean residence depends on population-specific ocean distributions and migration patterns (Larson et al., 2013; Weitkamp, 2010). Predation intensity is likely highest for coastal populations from Washington, British Columbia and south-eastern Alaska, somewhat uncertain for populations in western Alaska, and lowest for populations that do not exhibit the long coastal migrations such as those from California and southern Oregon, as well as some Puget Sound populations. This spatial pattern of exposure to predation is generally coherent with the observed patterns in the declining size of older Chinook salmon across the Pacific coast (Figures 7 and S4) and warrants more examination of the potential of increased predation for contributing to the changing demographic characteristics we have documented in this study.

5 | CONCLUSIONS

Chinook salmon are highly valued for their large size and nutritional value by humans and apex predators alike. Here, we report on the loss of the largest and oldest fish from many populations across the west coast of North America. Declines in size-at-age were found to be common coast-wide and were most pronounced in northern populations. The southernmost populations, in contrast, showed no or weak trends in size-at-age. Furthermore, while the loss of the oldest fish and corresponding decline in mean age was found for the majority of populations, trends in age compositions differed between regions. Most notably, populations from British Columbia for which we had data did not follow the decline in mean age.

Our qualitative assessment of the potential causes of changes in age-size structure suggests that common hypotheses such as harvest, environmental change and hatchery effects are not consistent with nor sufficient to explain observed patterns of demographic change in Chinook salmon observed across space and time. The causes of the declining size and age trends are likely complex and involve multiple factors that may interact. Changes in predation rates on the oldest and largest fish by expanding populations of resident killer whales is a

hypothesis that appears largely consistent with the observed changes, but it remains untested. In the light of the presented findings, this and other hypotheses should be evaluated in more detail in future studies before firm conclusions about the underlying causes can be drawn.

ACKNOWLEDGEMENTS

Funding for this project was provided by the Cook Inlet Salmon Disaster Technical Committee through the Pacific States Marine Fisheries Commission. We thank Mark Scheuerell, Bill Templin, Andrew Munro, Dani Evenson and two anonymous reviewers for helpful comments on an earlier version of this manuscript. We further thank Tim Walsworth, Thomas Buehrens and Tim Cline for inspiring discussions and Thomas Buehrens for help gathering data.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Ohlberger J, Ward EJ, Schindler DE, Lewis B. Demographic changes in Chinook salmon across the Northeast Pacific Ocean. *Fish Fish*. 2018;00:1–14. <https://doi.org/10.1111/faf.12272>



Resurgence of an apex marine predator and the decline in prey body size

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Edited by James A. Estes, University of California, Santa Cruz, CA, and approved November 13, 2019 (received for review June 25, 2019)

In light of recent recoveries of marine mammal populations worldwide and heightened concern about their impacts on marine food webs and global fisheries, it has become increasingly important to understand the potential impacts of large marine mammal predators on prey populations and their life-history traits. In coastal waters of the northeast Pacific Ocean, marine mammals have increased in abundance over the past 40 to 50 y, including fish-eating killer whales that feed primarily on Chinook salmon. Chinook salmon, a species of high cultural and economic value, have exhibited marked declines in average size and age throughout most of their North American range. This raises the question of whether size-selective predation by marine mammals is generating these trends in life-history characteristics. Here we show that increased predation since the 1970s, but not fishery selection alone, can explain the changes in age and size structure observed for Chinook salmon populations along the west coast of North America. Simulations suggest that the decline in mean size results from the selective removal of large fish and an evolutionary shift toward faster growth and earlier maturation caused by selection. Our conclusion that intensifying predation by fish-eating killer whales contributes to the continuing decline in Chinook salmon body size points to conflicting management and conservation objectives for these two iconic species.

age and size structure | fisheries | life-history traits | predation | evolutionary change

Large marine mammal predators can have pronounced effects on marine ecosystems, primarily because of their mobility, size, and high energy demand (1), especially at higher latitudes (2). It is well established that large predators can critically affect food web structure and function, including direct effects on prey populations and indirect trophic cascades (1, 3, 4). However, the implications of changing predation pressure for prey life-history characteristics and phenotypic traits remain poorly understood. This is surprising given mounting evidence for fishing-induced trait changes in harvested populations (5–7) and is particularly important in light of recent conservation efforts leading to recoveries of many large marine mammal populations worldwide. The recoveries have heightened concerns for the potential impacts of apex predators on global fisheries, thus creating new trade-offs for natural resource management and conservation (8, 9).

Chinook salmon (*Oncorhynchus tshawytscha*) are anadromous fish that hatch and rear in freshwater, subsequently migrate to sea to spend 1 to 5 y in the ocean, and finally return to their natal rivers to spawn once and then die (10). In the ocean, these fish often migrate thousands of kilometers and are widely distributed along the west coast of North America, the Gulf of Alaska, and farther west along the Aleutian Islands and into the Bering Sea (11, 12). Chinook salmon have exhibited marked shifts in demographic structure throughout most of the North American range over the past 4 to 5 decades (13–16). In most populations, fish now mature at younger ages, and while the size of younger fish has been stable or increasing, older fish that return to spawn after several years in the ocean are increasingly smaller. In other

words, size at age is declining for older fish but not for younger fish. As a result, the contributions of the largest and oldest fish to populations have declined since the 1970s, a trend that is remarkably consistent among populations (14) along the west coast of North America. The trend toward smaller and younger fish is a pressing concern because Chinook salmon are valuable to commercial, recreational, and subsistence fisheries, and because large fish contribute disproportionately to reproduction. Causes of the observed changes in demographic characteristics have remained elusive, although effects of harvesting, including evolutionary changes, have been hypothesized for decades (17). The widespread loss of the oldest and largest fish indicates a common driver operating at basin-wide spatial scales that has been changing through time. One potential basin-wide driver is the coast-wide recovery of marine mammal predators following successful implementation of the 1972 US Marine Mammal Protection Act.

Killer whales (*Orcinus orca*) are the ocean's ultimate apex predator and are widely distributed throughout the world's oceans. In the northeast Pacific Ocean, three ecotypes are distinguished based on their diet: fish-eating “residents,” mammal-eating “transients,” and “offshore” killer whales that eat fish and other organisms. Resident killer whales, which primarily occupy coastal waters, have nearly tripled in abundance in the northeast Pacific Ocean (18) since the early 1970s (19, 20). Their diets are dominated by salmon, especially Chinook salmon, which have the highest energy content of any salmon, and the whales selectively prey on the largest Chinook salmon (21–24). Killer whales are

Significance

Recent recoveries of marine mammal populations worldwide have heightened concerns for their potential impacts on global fisheries. While predator-induced reductions in prey abundance have been documented, trait-mediated changes in life-history characteristics are rarely considered. Here we provide a striking example of the impact of a resurging apex marine predator on a commercially important fish species through changes in prey life-history traits. We find that widespread declines in the body size of Chinook salmon over the past 50 y can be explained by intensified predation by growing populations of resident killer whales that selectively feed on large Chinook salmon, thus revealing a potential conflict between salmon fisheries and marine mammal conservation objectives.

Author contributions: J.O., D.E.S., E.J.W., T.E.W., and T.E.E. designed research; J.O. performed research; J.O. analyzed data; and J.O., D.E.S., E.J.W., T.E.W., and T.E.E. wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission.

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This article contains supporting information online at <https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.1910930116/-DCSupplemental>.

estimated to currently consume over 2.5 million adult Chinook salmon each year (23). Because of declines in fisheries' harvests since the 1980s, these consumption levels by killer whales now exceed the combined annual removals of Chinook salmon by commercial, recreational, and subsistence fisheries (23).

We investigated the potential role of fisheries harvest and predation by growing populations of fish-eating killer whales in causing the shift in demographic structure that has led to precipitous declines in the mean size of Chinook salmon (14). Size-selective predation and fishing both act to alter the age and size composition of prey populations via direct removals and selection for evolutionary changes in life-history traits related to growth and maturation. Over the past 50 y, changes in fishery exploitation of Chinook salmon have occurred independently of the temporal patterns of change in killer whale populations, thus allowing us to distinguish potential effects of each source of mortality on Chinook salmon demographic structure. We developed an age- and size-based population model for Chinook salmon that allowed for the evolution of individual growth trajectories and maturation (*Materials and Methods*). *SI Appendix* contains details on the timing of life-history events, model functions, and parameters (*SI Appendix*, Figs. S1 and S2 and Table S1). We evaluated patterns of predation pressure (intensity and size selectivity) that would be expected to cause changes in the body size of returning Chinook salmon similar to observed size declines given multidecadal changes in fishery harvest rates and contrast these against scenarios without predation or fishing mortality. Our model mimics historical changes in harvest rates and recent increases in predation rates due to a growing number of fish-eating killer whales (*SI Appendix*, Fig. S3). For the past 50 y, the time period during which reliable empirical data were collected, harvest declined and predation pressure increased (23, 25); we evaluate changes in size at age, age composition, and overall mean body size and compare these to observed changes for Chinook salmon along the west coast of North America (Fig. 1) (14).

Results and Discussion

Model simulations revealed that an increasing rate of size-selective predation is necessary to generate the strong demographic shifts in size at age, age composition, and mean body size observed in North American Chinook salmon since the 1970s. Our results suggest that fish-eating killer whales are currently having a larger effect than fisheries on phenotypic traits and life-history characteristics of Chinook salmon. Further, the direct removal of large maturing fish, primarily via predation, has a larger effect on prey body size than evolutionary changes resulting from selection for faster growth and earlier maturation. Below we detail the results supporting these claims.

The simulated trends toward smaller and younger individuals in the escapement (Fig. 2), that is, fish that have matured and survived predation and fishing mortality, matches the broad-scale patterns observed in many North American Chinook salmon populations (14). The change in mean size is not linear over time but suggests that mean body size declined particularly rapidly during the late 1970s and again since the late 1990s brood years. The model reproduces observed changes in age composition and size at age of spawners over the past few decades, with increasing proportions and size at age of younger ages and declining proportions and size at age of older ages (Fig. 1 and *SI Appendix*, Fig. S4) (14). These shifts in age composition and size at age result in marked declines in overall mean body size, as seen in both our model simulations (Fig. 2) and the empirical data which suggest declines in mean body length of at least 70 mm (~9%) between brood years 1971 and 2009 (Fig. 1).

Both removals of large, old individuals and evolutionary changes in growth and maturation contribute to changes in mean size in the escapement. We simulated declines in mean size using

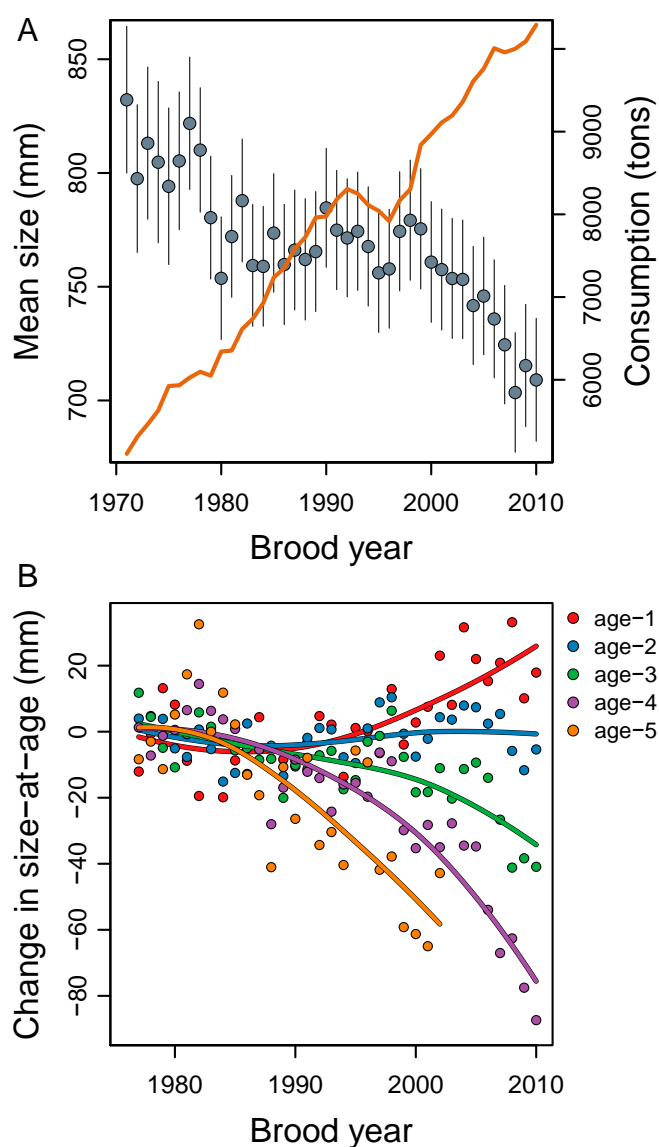


Fig. 1. Estimated changes in mean size, size at age, and consumption of Chinook salmon along the west coast of North America. (A) Estimated annual mean lengths of Chinook salmon (blue circles) with 90% confidence intervals (bars) and estimated biomass of Chinook salmon consumed in each year by "resident" fish-eating killer whales (orange line), as reported in ref. 23. Consumption estimates were lagged by 5 y to match the brood year of Chinook salmon (years when eggs of a certain cohort of fish were deposited in the gravel). (B) Estimated changes in mean size at age of Chinook salmon (circles; LOESS [locally estimated scatterplot smoothing] smoothers indicate temporal trends) for ocean ages 1 (red), 2 (blue), 3 (green), 4 (purple), and 5 (orange) from linear mixed effects models using the approach presented in ref. 14. Sample sizes by age group prior to 1975 were not sufficient for inclusion in these models. Estimates of changes in Chinook salmon body size were made for fish that have returned to freshwater habitats to spawn and were considered part of the escapement.

a model with and without evolution in growth and maturation traits (Fig. 3) and found declines in mean size to be largest in the evolutionary model (8 to 9% decline, default parameters) with a roughly 1.5 times stronger decline in mean size compared to a model without evolution (5 to 6% decline). This result suggests that evolutionary changes toward smaller maximum size, faster early growth, and maturation at younger ages contribute to declining average sizes, although they might be less important than

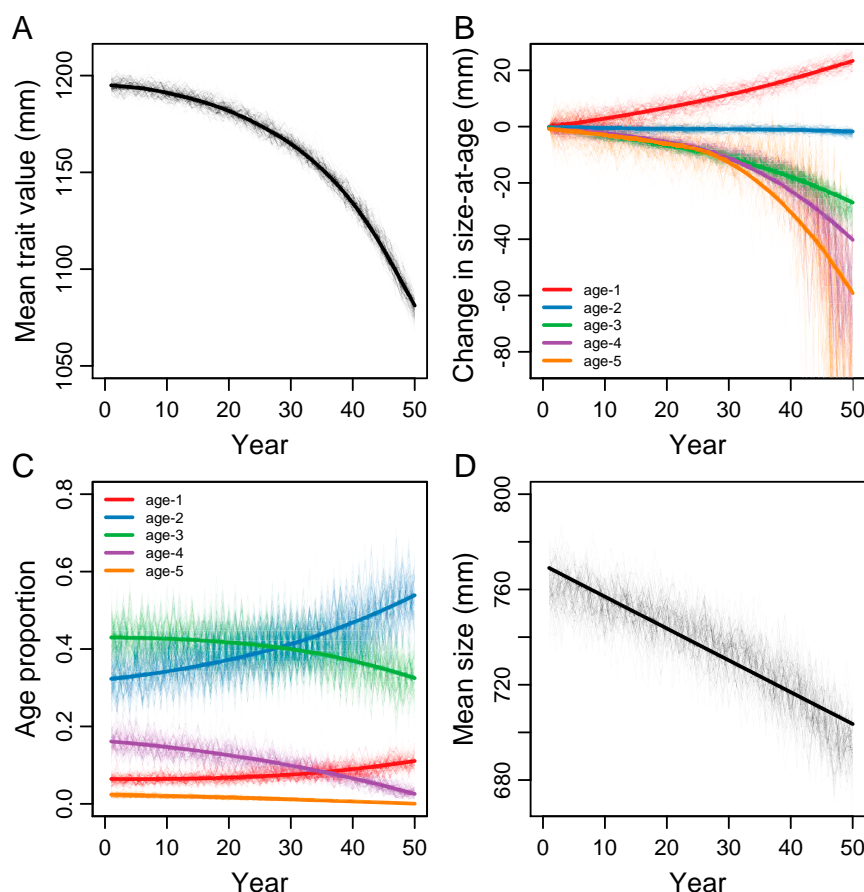


Fig. 2. Simulated changes in age-size structure of Chinook salmon. Shown are changes in the age and size composition of the escapement (fish that have matured and survived predation and fishing mortality) based on 100 stochastic runs using default parameter values. The panels show (A) mean trait value (average asymptotic length), (B) change in size at age (relative to initial size), (C) age proportions, and (D) overall mean size. Smooth lines indicate temporal trends using LOESS smoothers fit to median values across stochastic runs. Colors refer to ages 1 (red), 2 (blue), 3 (green), 4 (purple), and 5 (orange).

the direct effects of selective removal by fisheries and apex predators. Evolution in the model simultaneously affected the growth and maturation processes due to an assumed correlation between asymptotic size and the maturation reaction norm, whereby a negative trait correlation implies that smaller maximum sizes result in earlier maturation. This is in line with empirical evidence suggesting that age and size at maturity are heritable traits in Chinook salmon (26, 27) and that the age threshold for maturation in North American Chinook salmon has declined in recent decades (28) coincident with declines in maximum size (14).

Our results suggest that adaptive evolution toward earlier maturation has contributed to life-history changes in Chinook salmon over the past few decades, as has been seen with the rapid evolution in age at maturity in other salmonids, for example Atlantic salmon (29). The pace of evolutionary change depends on the strength of selection and on heritability in size- and age-related traits. Heritability is the proportion of phenotypic variation attributable to genetic variation among individuals. In our model, it is determined by the trait variance and the variance in growth rate (*SI Appendix, Fig. S5*), which were set such that heritability was similar to values reported for size- and age-related traits in Chinook salmon (27, 30, 31). Nonevolutionary dynamics were simulated by setting the trait variance to zero, such that no trait evolution could occur, and changes in mean size of the escapement would be caused exclusively by selective removals of mature individuals.

Size-selective predation on large individuals has immediate effects on the age and size composition of returning fish and may

select for evolutionary shifts in growth-related traits. Predation mortality disproportionately affected older fish that had grown to larger body sizes and thus caused the strongest decline in size at age among the oldest fish. Size-selective predation predominantly removes larger individuals of a certain age as long as selectivity increases with body size over the range of prey sizes present in that age group. Our simulations revealed that the

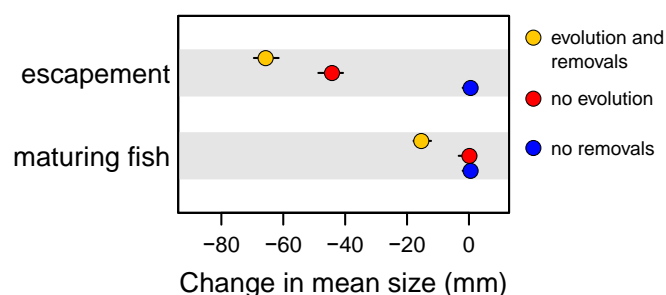


Fig. 3. Changes in mean size of Chinook salmon when omitting evolution or removals. Shown are changes in mean size for the escapement (upper band) and maturing fish (lower band) over the last 50 y for the model including removals and allowing for trait evolution (yellow) and simulations either omitting evolution (red) or omitting any size-selective removals (blue). Circles represent median values and bars represent 5th and 95th percentiles of 100 stochastic runs.

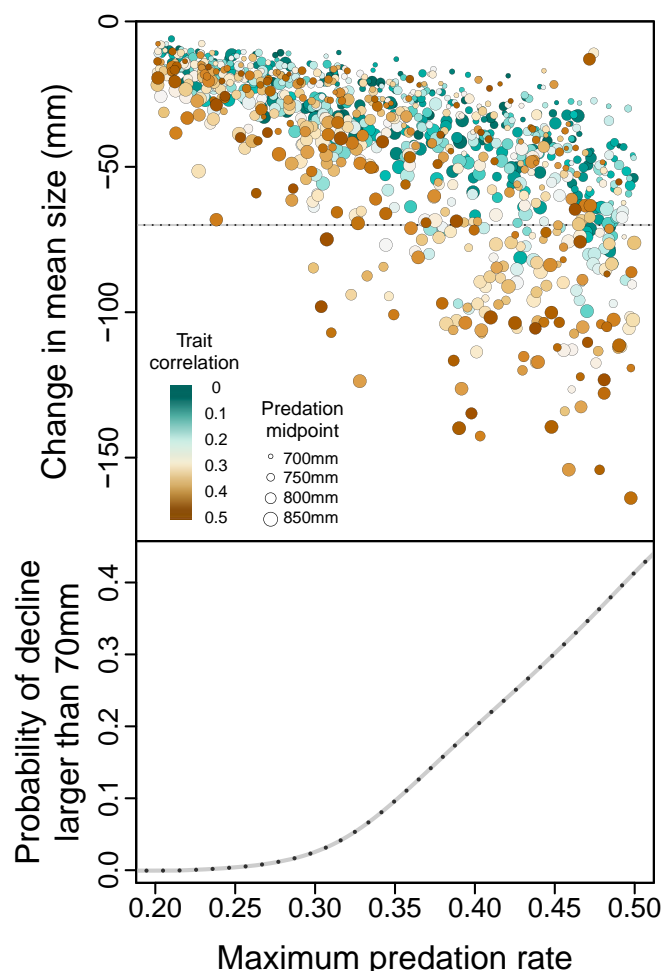


Fig. 4. Change in mean size of Chinook salmon as a function of maximum predation rate based on random permutations of model parameters. (Top) The decline in mean size as a function of maximum predation rate for 1,000 simulations based on randomly drawn parameter values. The empirically estimated size decline of at least 70 mm is indicated by the horizontal line. The size and color of circles reflect the relative values of the two other most important parameters affecting changes in mean size: the predation midpoint (size of circles) and the trait correlation between growth and maturation (color of circles). (Bottom) Results from a quantile regression of simulated size changes that was used to estimate the probability of a size decline of at least 70 mm (threshold) as a function of maximum predation rate.

trend in mean size of the escapement was highly sensitive to predation parameters, specifically the predation rate and midpoint of the size selectivity function (*SI Appendix, Fig. S6*). Declines in mean length on the order of those observed for Chinook salmon populations coast-wide over the past 40 to 50 y (at least 70 mm, or ~9%) were only reproduced with a predation rate of 0.3 or higher toward the end of the simulation (Fig. 4). Based on simulations where all model parameters were drawn randomly from a specified range of reasonable values, the probability of a decline in mean size larger than the 70-mm threshold was 2.5% at a maximum predation rate of 0.3 (Fig. 4) but rapidly increased and reached a probability of over 40% at a maximum predation rate of 0.5 (the full set of responses for the most important parameters is shown in *SI Appendix, Fig. S7*). Therefore, if more than 30% of maturing Chinook salmon are currently being consumed by fish-eating killer whales, a size decline on the order of that observed in the empirical data is plausible, and the decline is likely to continue in the future.

Other marine mammals that have increased in abundance (18), including pinnipeds, also feed on Chinook salmon. Harbor seals (*Phoca vitulina*) can significantly reduce Chinook salmon marine survival (23, 32); however, these predators primarily target Chinook salmon during their residency in estuaries or first year at sea and are not thought to feed selectively on large fish. Yet, lower abundances due to increased early ocean mortality may exacerbate the impact of size-selective predation later in life and may result in a release from competition for resources, thus contributing to changes in growth rates. California sea lions (*Zalophus californianus*) and Steller sea lions (*Eumetopias jubatus*) may target adult Chinook salmon, although consumption from these predators is thought to be a fraction of that consumed by fish-eating killer whales, in part because Chinook salmon represent a small fraction of sea lions' diets. Increasing abundances of other marine predators such as salmon sharks (*Lamna ditropis*) could also be compounding the effects of predation by killer whales if their selectivity patterns are similar and their abundance is large enough to significantly reduce the survival of large Chinook salmon (33–35). Importantly, killer whales are highly selective for the largest fish and are estimated to consume several times more Chinook salmon biomass than other predators (23). We therefore focused our assessment on size-selective predation by fish-eating killer whales.

Fisheries often exert selection on life-history traits by selectively removing larger individuals, and evidence for fishing-induced evolution in exploited species is mounting (5–7, 36, 37). Harvesting had a weaker effect on changes in mean body size of Chinook salmon compared to predation, because harvest rates have declined in recent decades while predation pressure has increased (*SI Appendix, Fig. S3*). Additional model simulations without predation mortality revealed that harvesting alone cannot explain the observed declines in body size of Chinook salmon over the past 50 y, and that the impacts of harvesting were likely stronger during the decades preceding the most recent period for which reliable empirical estimates of changes in mean body size of Chinook salmon exist (*SI Appendix, Fig. S8*). Sufficiently strong harvest rates and selectivity may have caused significant declines in mean size during earlier periods (*SI Appendix, Fig. S9*).

Commercial fisheries for Chinook salmon in coastal waters of the northeast Pacific developed during the late 19th and early 20th century. From the 1920s to the 1970s, harvest removals by commercial fisheries were relatively stable, when each year between 2.2 and 3.8 million fish were captured in commercial fisheries (38). After the late 1970s, harvests of Chinook salmon started to decline, while the production of hatchery-origin fish increased rapidly (38), such that harvest rates were highest prior to the 1970s and have declined since (25, 39, 40). These patterns of changes in fishery exploitation are not concordant with the observed changes in Chinook salmon life history characteristics observed in the last 50 y (14).

Harvest-induced size declines would be expected to continue for multiple generations only in populations that continue to experience sustained or increasing harvest levels. Yet, despite reductions in harvest rates in many populations (25, 41, 42), Chinook salmon continue to return at smaller sizes and younger ages throughout most of their North American range, and size declines have been most pronounced during the last 15 y. Furthermore, size trends are similar in geographically close populations that experience differential fishing pressure and/or selection regimes, as reported for Chinook salmon in Alaska (43). It is also noteworthy that mean body weights of other Pacific salmon have generally declined less than those of Chinook salmon since the mid-20th century, and these species have also been heavily exploited by fisheries (38, 44). Trends toward smaller mean weight in fishery catches of North American Chinook salmon during the 1950s to 1970s were reported almost 40 y ago (45), although it remained speculative to what extent declines in mean catch weight were

caused by harvesting. Our results suggest that the main impact of fishing on the size and age composition of Chinook salmon indeed occurred prior to the 1970s (*SI Appendix*, Fig. S8). Size declines likely continued because the combined removals by fisheries and marine mammal predators have increased continuously over the past century (23, 40). Without increasing predation pressure, average sizes of Chinook salmon should have partly recovered due to reductions in fisheries harvest during the past 40 to 50 y (*SI Appendix*, Fig. S9). To our knowledge, data that would allow reconstruction of average body sizes have not been collected systematically prior to the onset of commercial fishing (but see ref. 46), such that we cannot make inferences about longer-term trends in Chinook salmon body size. However, current population sizes of Chinook salmon are very likely much lower compared to pre-modern times, which could facilitate pronounced effects of size-selective predation compared to previous times when marine mammals may have been abundant, because the magnitude of the predation effect also depends on the abundance of prey (47).

In addition to size-selective predation and harvest mortality, changes in growth conditions at sea can affect the size at age and maturation of Chinook salmon. The growth environment experienced by Chinook salmon in the ocean has clearly changed over the past decades (14), and variation in the slope of change in mean size (Fig. 1) indicates that other factors have contributed to changing demographic structure. While slower growth due to lower ocean productivity or increased competition with other salmonids could contribute to declining size at age of older fish, this is expected to result in later maturation in semelparous Pacific salmon, because slow-growing individuals mature later than fast-growing individuals (48, 49). The observation for Chinook salmon that age at maturation declined along with the size at age of older fish (14) contrasts with other semelparous species such as chum salmon (*Oncorhynchus keta*) (45, 48) and sockeye salmon (*Oncorhynchus nerka*) (13, 50, 51), which have experienced stable or increasing age at maturation while size at age has declined. Fish-eating killer whales feed on other species of Pacific salmon, such as chum and coho salmon, though to a lesser extent (21–24).

The observation that the size at age of young Chinook salmon in the ocean has increased indicates that growth conditions during the salmon's first 1 or 2 y at sea have improved, or that the fish enter the ocean at larger sizes (14). More favorable growth conditions in the ocean could lead to accelerated growth early in life and thus earlier maturation. A potential mechanism causing faster growth is a release from competition, for instance caused by higher early ocean mortality of Chinook salmon due to increased harbor seal abundances (23). However, faster early growth due to higher food abundance is expected to also lead to larger size at age later in life (52, 53), unless feeding conditions continuously deteriorate as the fish grow, or size-selective mortality later in life selects for smaller maximum size. Finally, while increased temperature due to climate warming can cause life-history changes similar to those observed in Chinook salmon, temperatures in the northeast Pacific have not shown spatially consistent and continuously increasing trends over the past few decades (14). Nonetheless, temperature effects could be contributing to observed demographic shifts in Chinook salmon and were not explicitly modeled in this study.

Hatchery practices may have contributed to larger sizes early in life by producing faster-growing smolts that enter the ocean at larger average size (54). Previous work suggests that trends in size at age are similar for wild and hatchery-origin fish, and that wild populations that are not exposed to hatchery introgression or potential competition with hatchery stocks, such as Chinook salmon in western Alaska, have experienced similar declines in the size at age of older fish (14). Furthermore, coast-wide hatchery releases of Chinook salmon increased rapidly in the 1970s and 1980s but have declined steadily since the late 1980s. Changes in hatchery practices may contribute to trends in demographic

characteristics but cannot explain changes in populations that experience little or no competition and introgression from hatchery fish.

Our model was developed to represent the typical life history of North American Chinook salmon. It ignores differences in life-history strategies among populations and regional trends in demographic change, harvest rates, predation pressure, and environmental conditions. For instance, Chinook salmon populations differ in many aspects of their life history, including growth rate, maturation schedule, and marine distribution (11, 14, 55). Hatchery-origin Chinook salmon are only produced in large quantities in the central and southern regions, from California to British Columbia. Furthermore, exposure to killer whale predation depends on the abundances, ocean distributions, and migration routes of both predators and prey. Abundances of fish-eating killer whales have increased continuously over the past decades, with the exception of the southern resident population that inhabits the Salish Sea and coastal waters from California to Vancouver Island. Interestingly, Chinook salmon populations from California and southern Oregon that do not migrate far northward along the coast and likely experience less killer whale predation have shown weak trends in mean size and age (14). Finally, harvest rates have not declined uniformly across space. Because our model is not spatially explicit, it cannot distinguish regional differences in how factors such as predation, harvest, hatcheries, competition, and ocean conditions have affected the demographic structure of Chinook salmon. The model could serve as a starting point for population-specific models that explore how regional factors may have contributed to the coast-wide decline in Chinook salmon body size.

While increasing predation pressure is likely contributing to declining average sizes in Chinook salmon, some populations of fish-eating killer whales may in turn be negatively affected by reduced abundances and body sizes of their prey. A decline of ~10% in mean length, as indicated by our data, implies a reduction in caloric value of an average-sized Chinook salmon of about 30 to 40% (56). Food limitation may be one of the factors responsible for the recent decline in the abundance of the southern resident killer whales (SRKW; refs. 57–59), the only population of fish-eating killer whales in the northeast Pacific Ocean that is not thriving. This emphasizes the importance of considering the complex interactions between predators and their prey as well as intra- and interspecific interactions among predators. In particular, interactions between SRKW and the expanding populations inhabiting more northerly waters appears to be an important component of understanding the concerning demographic status of SRKW. Some Chinook salmon populations originating from central and southern parts of their North American range are protected under the US Endangered Species Act, and fish-eating killer whales are protected under the US Marine Mammal Protection Act and the Canadian Species at Risk Act (40, 60, 61). The potential trade-off between management objectives, namely maintaining or increasing abundances of both predators and their prey, poses a challenge to conservation. Fisheries management which provides harvest opportunities for tribal, subsistence, sport, and commercial fisheries, is faced with additional challenges due to the resurgence of marine mammal predators. It is thus important to acknowledge trade-offs between conservation and benefits to fisheries when determining management goals. Interestingly, protecting marine mammals by rebuilding fisheries is increasingly proposed as a target conservation strategy (62). Rebuilding salmon might be more challenging for populations that have experienced severe declines in mean size and thus spawner quality. If killer whales are causing changes in Chinook salmon demographics through undesirable changes in phenotypic traits that might propagate to affect population productivity and their fisheries, future conservation conflicts seem inevitable.

Materials and Methods

Data Analysis. The analysis of changes in body size of Chinook salmon relies on data for wild and hatchery populations from central California to western Alaska available in agency databases and the Regional Mark Information System (RMIS). Detailed descriptions for synthesizing these data for the purposes of size at age and age composition analyses can be found in a previous study (14). We fit linear mixed effects models to individual observations of size (fork length, in millimeters) of Chinook salmon covering the brood years 1971 to 2010. Chinook salmon have a complex life history with fish returning to spawn after 0 to 2 y in freshwater and 1 to 5 y in the ocean, meaning the fish returning in any given year represent a mix of fish originating from different brood years. Analyses of changes in mean size were performed by brood year, the years when eggs of a particular cohort of fish were deposited in the gravel, to avoid confounding effects of variation in year class strength of multiple returning cohorts in a given run year. We only used samples of individuals that were considered part of the escapement, that is, fish that have escaped the fisheries and returned to freshwater habitats to spawn (~900,000 samples). This was done to ensure that the results would not depend on the inclusion of potentially selective fishery data and that the estimated time series would reflect postremoval trends in mean size.

We considered the categorical fixed effects of brood year, rearing type (hatchery/wild), sampling method (fishery code, eight levels), run type (spring, summer, fall, late fall, upriver bright), and freshwater age (0, 1, 2) in the case of age-specific models, while day of year of sampling was considered as a continuous variable (for further details on the variables see ref. 14). Categories with at least five observations and populations with at least 5 y of data were included in the analysis. Random intercepts for each year nested within population were used to account for the lack of independence of data within years and populations. The mixed-effects models had the form $L_i = \beta_0 + \beta_1 FE_1 + \dots + \beta_n FE_n + b_{p|y} + \epsilon_i$, where β_0 is the intercept, β_1, \dots, β_n are regression coefficients of the fixed effects (FE), $b_{p|y} \sim N(0, \sigma_b^2)$ is a normally distributed random effect for year (y) nested in population (p), and $\epsilon_i \sim N(0, \sigma^2)$ is a normally distributed error term. Models were fit using the package nlme (v.3.1-128) (63) in R (v.3.5.1) (64). Inclusion of nested random effects was supported by a likelihood ratio test. Inclusion of fixed effects was determined using Akaike information criterion-based multimodel inference using the MuMIn package (v.1.24.1) (65) by evaluating the complete set of models with all possible combinations of fixed effects. Models with different fixed effects were compared using maximum likelihood estimation, and models with different random effects and the final model were fit using restricted maximum likelihood. The selected mean size model included all fixed effects but no interactions. Based on the selected model, year predictions were made for wild fall-run Chinook salmon.

Estimates of consumption by fish-eating killer whales were taken from a recent study on marine mammal predation of Chinook salmon (23) and were lagged by 5 y to match the brood year of Chinook salmon, because most fish consumed are 5 to 6 y old (Fig. 1).

Simulation Model. We simulate how changes in predation pressure and fishery exploitation would be expected to alter the age and size composition of returning Chinook salmon over time, with the main goal of identifying ecological conditions that might have caused demographic changes similar to those observed in North American Chinook salmon. Our dynamic age- and size-based population model for Chinook salmon allows for the gradual evolution of traits related to growth and maturation. Specifically, the asymptotic average size of individuals in the population and a correlated trait that determines the probability of maturing at a given age and size can evolve in response to changes in survival probability due to size-selective harvest and/or predation.

Model Functions and Parameters. The model functions and parameter values reflect the typical life history of Chinook salmon in the northeast Pacific Ocean. We defined a set of default parameter values based on available literature and empirical data on Chinook salmon, but our model analysis explores deviations in parameter values within ranges that were considered biologically reasonable (SI Appendix, Table S1), including simultaneous random draws of all model parameters.

Reproduction. Fecundity in Chinook salmon depends on female body size. The number of eggs (E) produced by a female was thus assumed to depend on female length (L) according to a power function $E = a_F L^{b_F}$, where a_F is the fecundity constant and b_F is the fecundity exponent (SI Appendix, Fig. S2). Parameter values were informed by literature data (66). Recruitment (R) of smolts was based on a 1:1 sex ratio in the population and depended on the

total number of eggs produced according to an asymptotic Beverton–Holt-type relationship, $R = E / \left(\frac{1}{a_R} + \frac{E}{b_R} \right) e^{\varepsilon_R}$, where a_R is the productivity and b_R is the capacity parameter of the density dependence function (SI Appendix, Fig. S2), and recruitment variability is assumed to be log-normally distributed with $\varepsilon_R \sim N(0, \sigma_R)$. Recruitment variability had a minor effect on trait dynamics and changes in mean size, and the default value was set to a moderate level of recruitment variation (67). The productivity parameter was based on literature values (10), and smolt capacity was set to ensure a sufficient number of individuals in each category to calculate statistical averages in any given year. Marine survival was assumed to be independent of population density.

Growth. The von Bertalanffy growth function was used to model individual growth. The growth increment ($g_{y,i}$) of individual i from 1 y (y) to the next is $g_{y,i} = k_i (L_{\infty,i} - L_{y-1,i}) e^{\varepsilon_G}$, where k_i is the growth rate coefficient (or growth rate), $L_{\infty,i}$ is the asymptotic average length (or maximum length), $L_{y-1,i}$ is previous length, and $\varepsilon_G \sim N(0, \sigma_G)$ describes growth variation due to stochastic environmental effects with variance σ_G (SI Appendix, Fig. S2). The length of individual i in year y is then $L_{y,i} = L_{y-1,i} + g_{y,i}$, where $L_{y-1,i}$ in the first year of life was defined as the average smolt length L_s . Annual growth increments were thus assumed to be stochastic and drawn from a lognormal distribution around the deterministic growth increment as determined by growth parameters k_i and $L_{\infty,i}$. Reference growth parameters were chosen such that the individual growth trajectories together with the age- and size-dependent maturation probabilities produced size distributions in the return that resembled the size distributions in the empirical data (14). The growth rate coefficient of an individual was further assumed to be correlated with the asymptotic average length, $k_i = k_{ref} - \beta_g L_{\infty,ref} + \beta_g L_{\infty,i}$, where $L_{\infty,ref}$ and k_{ref} are the reference values of maximum size and growth rate, respectively, and β_g is the slope of the relationship between the two parameters (SI Appendix, Fig. S2). The growth parameters trade-off was based on an estimated correlation between the two growth parameters using values reported in a stock assessment model used to manage Chinook salmon populations on the west coast of the United States and Canada (Fishery Regulation Assessment Model) (68). We thus assume that the range of possible individual growth trajectories is constrained by a trade-off between average asymptotic length and growth rate.

Evolution. The asymptotic average length was modeled as a quantitative trait that evolved gradually in response to selection due to size-dependent survival (and was assumed to be correlated to the maturation schedule, discussed below). Its initial value was set to approximate the equilibrium mean trait value under default values of all other parameters (10, 55). The evolutionary dynamics depend on the variances in asymptotic size and growth rate that together determine trait heritability, which was not a parameter in the model. Heritability was calculated as the amount of expected deterministic variance in size at age over the amount of stochastic variance in size at age for ocean age-1 fish (SI Appendix, Fig. S5), which was the age group least affected by size-selective removals. We assumed constant genetic variance in the population, which implies a time-invariant mutation–segregation–recombination kernel, as done elsewhere (69, 70). Offspring trait values were drawn from a normal distribution around the mean parental trait value with constant variance (truncated at zero), although recent evidence suggests that age at maturation in salmonids may be controlled by a single locus (29, 71). Variances in asymptotic size and growth rate were set to reflect heritability values for length- and age-related traits in Chinook salmon, which are typically around 0.20 to 0.35 (27, 30). The emergent heritability for size at ocean age 1 at equilibrium dynamics in our model (without fishing and predation) using default parameter values was around 0.22.

Maturation. The maturation process was modeled using a probabilistic maturation reaction norm. Probabilities of maturing at a given age (a) and size (s) are given by a logistic function, $P_{M,a,s} = 1 / \left(1 + \exp \left(- \frac{L - L_{M50,a}}{\sigma_M} \right) \right)$, where $L_{M50,a}$ are the reaction norm midpoints describing the age-specific lengths at which maturation probability is 50%, and σ_M determines the width of the reaction norm. The default value of the variance term σ_M was set to resemble the relative widths of reaction norms used in other studies (17, 72). The reaction norm midpoints are given by $L_{M50,a} = \alpha_M + \beta_M a$, where α_M and β_M are the intercept and slope (SI Appendix, Fig. S2), respectively. We assumed a negative slope of the maturation reaction norm such that faster-growing fish mature at a younger age compared to slower-growing fish, in line with other studies (17, 48, 49). Default values were set such that the resulting proportions of maturing individuals were in line with the literature (17, 73) and resembled typical age proportions of maturing fish with ocean ages 2 to 4 being the dominant age groups in the return (14). The maturation reaction norm intercept α_M was correlated to maximum size, $\alpha_{M,i} = \alpha_{M,ref} - \gamma (L_{\infty,ref} - L_{\infty,i})$, where $\alpha_{M,ref}$ is the reference intercept and γ is

the slope of the relationship (SI Appendix, Fig. S2). While there is evidence for sex-specific evolution of age and size at maturity in salmonids (29, 71), trait evolution in our model was not sex-specific and we assumed that the resulting evolutionary changes reflect average trait changes of both sexes. We modeled trait changes in the reaction norm intercept because available studies suggest that evolution is more likely to shift the intercept than the slope of the maturation reaction norm (72). Because the strength of the trait correlation was uncertain, we tested a wide range of values, ranging from no correlation to a strong correlation that would imply rapid evolution of the maturation schedule with changes in maximum size (SI Appendix, Table S1).

Survival. Size-independent annual survival was assumed to be low during the first year at sea and relatively high in subsequent years of marine residence (74, 75). Size-dependent survival due to size-selective predation and harvest occurred after maturation.

Predation removals were based on the predation rate in a given year (PR_y) and the size selectivity of predation ($S_{P,S}$). Selectivity was modeled as a sigmoid function given by $S_{P,S} = 1 / (1 + \exp(-\beta_P(L - L_{P50})))$, where L_{P50} is the selection midpoint at which selectivity is half of its maximum, and β_P determines the steepness of the selectivity curve (SI Appendix, Fig. S2). The selectivity parameters were based on available data of killer whales feeding on Chinook salmon (76) and selectivity curves estimated from those data (25). Because the selectivity function was estimated from empirical data, other functional forms were not tested. This logistic form is flexible in allowing a wide range of selectivity patterns, from gradual to knife-edge, and we explore a wide range of values for the midpoint and steepness. Predation rate was simulated to increase over the last 50 y of the simulations. We tested a wide range of plausible predation rates (SI Appendix, Table S1). Observed size declines could also result from the accumulating effects of selection under constant predation (SI Appendix, Fig. S10); however, this scenario was considered highly unlikely, because predator abundances have increased continuously over the past few decades (23).

Harvest removals were based on the harvest rate in a given year (HR_y) and the size selectivity of harvest ($S_{H,S}$). Harvest selectivity was modeled as a unimodal function with specified variances to reflect different degrees of selectivity, $S_{H,S} = \exp(-(\ln(L) - \ln(L_{H,max}))^2 / 2\sigma_H^2)$, where $L_{H,max}$ is the length at maximum selectivity and σ_H is the SD on log scale, which determines the

degree of selectivity (SI Appendix, Fig. S2). We used a value of $\sigma_H = 0.25$ to represent a selective (gillnet) fishery, a value of $\sigma_H = 0.5$ to represent a mixed (troll, gillnet, and seine) fishery, and a value of $\sigma_H = 2$ to represent a largely unselective (troll) fishery. The unimodal form was based on previously estimated selectivity curves for Chinook salmon gillnet fisheries, where the length at maximum selectivity resembled different mesh sizes used in typical gillnet fisheries, with values of 625, 725, and 825 mm representing 6.5-, 7.5-, and 8.5-inch mesh sizes, respectively (77). We tested a wide range of harvest rates (SI Appendix, Table S1).

Model Simulations. The simulation model tracks individuals of a given age, size, and trait in each year and by "state" (immature, mature, preyed upon, returned, harvested, and escaped). We discretized the size and trait space using a resolution of 10 mm and model five ocean age groups, where the oldest is a plus group such that individuals that do not mature by ocean age 5 (less than 0.1% of a given cohort) remain in this age group until they reach maturity. Space is implicit in the model: Reproduction and density-dependent juvenile survival occur in freshwater, somatic growth and maturation occur during ocean residence, and predation and harvest mortality occur after maturation during the return migration, prior to reproduction in freshwater habitats. Each year individuals grow, experience size-independent mortality, some individuals in each age group reach maturity, and these individuals subsequently experience size-dependent predation and fishing mortality, or escape to reproduce and then die. Details of how the model keeps track of individuals by age, size, trait, and state are provided in SI Appendix, Supplementary Methods: Model Simulations.

Code for the simulation model is available from the corresponding author upon request. Data used to analyze changes in Chinook salmon body size were presented in an earlier study (14), available from the RMIS (<http://www.rmish.org/>) and the respective state agencies (Alaska Department of Fish and Game and Washington Department of Fish and Wildlife).

ACKNOWLEDGMENTS. We thank Brandon Chasco for help throughout the project. Comments by Michael Ford, Brandon Chasco, and three anonymous reviewers helped to improve this manuscript. Funding was provided by the Pacific States Marine Fisheries Commission and the North Pacific Research Board.

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CERTIFICATE OF SERVICE

I hereby certify that on May 11, 2020, I served the foregoing **DECLARATION OF DR. DANIEL SCHINDLER IN SUPPORT OF DEFENDANT-INTERVENOR ALASKA TROLLERS ASSOCIATION'S BRIEF IN OPPOSITION TO PLAINTIFF'S MOTION FOR PRELIMINARY INJUNCTION** on the following individual(s):

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- ☒ by the Court's CM/ECF system to the email addresses listed above
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s/ Kathy Baker

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